

**Salmon Life Histories, Habitat, and Food Webs in the Columbia River Estuary:
An Overview of Research Results, 2002-2006**

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Report of research by

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for

Portland District
Northwestern Division
U.S. Army Corps of Engineers
P.O. Box 2946
Portland, Oregon 97208-2946
Contract No. W66QKZ 7007 8056

and

Environment, Fish, and Wildlife Division
Bonneville Power Administration
U.S. Department of Energy
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August 2008

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EXECUTIVE SUMMARY

From 2002 through 2006 we investigated historical and contemporary variations in juvenile Chinook salmon *Oncorhynchus tshawytscha* life histories, habitat associations, and food webs in the lower Columbia River estuary (mouth to rkm 101). At near-shore beach-seining sites in the estuary, Chinook salmon occurred during all months of the year, increasing in abundance from January through late spring or early summer and declining rapidly after July. Recently emerged fry dispersed throughout the estuary in early spring, and fry migrants were abundant in the estuary until April or May each year. Each spring, mean salmon size increased from the tidal freshwater zone to the estuary mouth; this trend may reflect estuarine growth and continued entry of smaller individuals from upriver.

Most juvenile Chinook salmon in the mainstem estuary fed actively on adult insects and epibenthic amphipods *Americorophium* spp. Estimated growth rates of juvenile Chinook salmon derived from otolith analysis averaged 0.5 mm d^{-1} , comparable to rates reported for juvenile salmon *Oncorhynchus* spp. in other Northwest estuaries. Estuarine salmon collections were composed of representatives from a diversity of evolutionarily significant units (ESUs) from the lower and upper Columbia Basin. Genetic stock groups in the estuary exhibited distinct seasonal and temporal abundance patterns, including a consistent peak in the Spring Creek Fall Chinook group in May, followed by a peak in the Western Cascades Fall Chinook group in July. The structure of acanthocephalan parasite assemblages in juvenile Chinook salmon from the tidal freshwater zone exhibited a consistent transition in June. This may have reflected changes in stock composition and associated habitat use and feeding histories.

From March through July, subyearling Chinook salmon were among the most abundant species in all wetland habitat types (emergent, forested, and scrub/shrub) surveyed in the lower 100 km of the estuary. Salmon densities within wetland habitats fell to low levels by July, similar to the pattern observed at mainstem beach-seining sites and coincident with high water temperatures that approached or exceeded 19°C by mid-summer. Wetland habitats were used primarily by small subyearling Chinook salmon, with the smallest size ranges (i.e., rarely exceeding 70 mm by the end of the wetland rearing season) at scrub/shrub forested sites above rkm 50. Wetland sites of all types were utilized by a diversity of genetic stock groups, including less abundant groups such as Interior Summer/Fall Chinook.

Juvenile salmon fed actively within wetland channel habitats. Salmon consumption rates in the Russian Island emergent wetland ranged from 11.3% body

weight in 2005 to 19.3% body weight in 2006. Estimated specific growth rates of salmon derived from recaptures of marked fish in the emergent wetland channel averaged 0.67 mm d^{-1} , similar to the otolith-derived estimates for individuals in the mainstem estuary. Studies of prey availability and salmon diets indicated that tidal wetlands are a major source of prey for juvenile Chinook salmon both within and outside wetland habitats. Insects produced in wetlands and other shallow habitats were utilized by salmon throughout the estuary, including larger size classes of fish that do not typically reside in wetland channels.

Analysis of historical habitat distributions in a Geographical Information System indicated that scrub/shrub and forested wetland types have declined in the estuary since the late 19th and early 20th centuries by 55 and 58%, respectively. Diking, filling, and other changes have reduced the total area of all wetland types combined from approximately 155 to 75 km^2 . Estimated loss of wetland habitat has been particularly high in the upper portion of the study area above Cathlamet Bay. Results of simulation modeling suggest that a combination of diking and flow regulation has fundamentally altered the dynamics of river/floodplain interactions in the tidal freshwater region above Cathlamet Bay, eliminating the opportunity for salmon to access the extensive tidal floodplain area.

Wetland losses have not only reduced the availability of shallow peripheral rearing habitats, but also have eliminated an important carbon source for salmonid food webs. Stable isotope analyses indicated that contemporary salmon select disproportionately for food webs linked to vascular plants and benthic diatoms, most likely through their consumption of prey resources produced in wetlands and other shallow-water habitats. These results suggest that reduced sources of macrodetritus from removal of tidal wetlands could undermine the estuary's capacity to support juvenile salmon. Increased water temperatures in the tidal freshwater region of the estuary since 1950 (from climatic changes and heating of mainstem reservoirs) have increased bioenergetic demands on salmon and may further constrain estuarine rearing opportunities, particularly during summer and fall months.

Together, changes throughout the basin (e.g., hatchery programs, population losses, flow regulation) and in the estuary (e.g. wetland habitat losses, increased water temperatures) may have decreased the proportion of Chinook salmon using the estuary during summer and fall months compared with the patterns observed during the first salmon life history study in 1916. These results support the hypothesis that life history diversity of Columbia River salmon has diminished since early in the 20th century and could limit the resilience of salmon populations to future environmental change. Of

particular concern are predicted regional effects of global warming that could place additional constraints on estuarine rearing opportunities, particularly in summer and fall.

Despite substantial estuarine habitat loss and evidence of reduced diversity of juvenile life histories, results from otolith, mark-recapture, and stable isotope studies confirmed that Chinook salmon throughout the Columbia River Basin rear in the estuary. With the likely exception of spring-run fish from interior basin ESUs, which may rarely occupy shallow estuarine habitats, Chinook salmon from all Columbia River ESUs with subyearling life histories reside in the estuary for extended periods, utilize a diversity of alternative habitat pathways, and interact with wetland food webs for periods of weeks to months. Extensive use of estuarine habitats by Chinook salmon suggests that actions above Bonneville Dam alone cannot satisfy salmon recovery goals and that populations throughout the basin would benefit from estuarine habitat restoration.

Recovery of Columbia River salmon will require that sufficient habitat opportunity is provided in the estuary to accommodate the full complement of stocks and life history types in the basin. Accordingly, a primary objective of salmon management and habitat restoration in the estuary should be to increase the diversity, extent, and spatial distribution of habitats capable of supporting multiple salmon ESUs and life history types. Among the principal concerns for salmon recovery programs in the estuary are

- 1) losses of peripheral wetland and tidal floodplain habitats;
- 2) effects of hatchery programs and hydropower and transportation operations on estuarine patterns of salmon abundance, migration, residency, and habitat use;
- 3) the risk of increasing water temperatures on summer and fall rearing opportunities for juvenile salmon.

In lieu of the present ad hoc approach to habitat restoration, estuary-wide strategic planning is needed to direct limited recovery resources toward those geographic areas, habitats, and activities that will most benefit multiple salmon ESUs. Recovery efforts should encompass the entire habitat continuum, not just sites in the lower estuary, where most research and restoration activities have been focused. Additional research is needed in the tidal freshwater region of the estuary above rkm 101 to understand habitat-use patterns across the entire estuarine tidal gradient for all genetic stock groups. At the same time, a few indicator sites should be established in the lower estuary to monitor the status and trends of juvenile migrants (e.g., life histories, abundance, size composition, genetic structure) and to provide indices of basin-wide salmonid response to the Columbia River Basin Fish and Wildlife Program.

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INTRODUCTION

In response to a 1998 estuarine research initiative of the Northwest Power Planning Council, a research team organized by NOAA Fisheries Service reviewed the current status of knowledge about the estuary's role in the life history and ecology of Columbia River salmon *Oncorhynchus* spp. The resulting report, *Salmon at River's End: The Role of the Estuary in the Decline and Recovery of Columbia River Salmon*, or SARE (Bottom et al. 2005), concluded that changes in the historical habitat of the estuary had reduced estuarine rearing opportunities for subyearling Chinook salmon *O. tshawytscha*. These changes included widespread removal of wetland and shallow-water habitat and the effects of flow regulation at mainstem dams. The authors hypothesized that these modifications, together with other disturbances in the basin, had reduced the diversity of salmon life histories, which could undermine population resilience to changing environmental conditions (Healey 1991; Thorpe 1994).

Other evidence suggested that estuarine habitat loss and the creation of storage reservoirs behind Columbia River dams also may have modified estuarine food webs to favor pelagic prey species, undermining the capacity of the estuary to support juvenile salmon (Bottom and Jones 1990; Sherwood et al. 1990). Unfortunately, because estuarine habitat use by Columbia River salmon has not been monitored consistently or comprehensively, few data exist to interpret the effects of estuarine modifications on historical populations or to draw inferences about the responses of at-risk salmon stocks to estuary restoration.

Traditional salmon management and recovery programs in the Columbia River basin have focused almost entirely on non-tidal habitats. Most estuarine surveys have been conducted for short periods and were often linked to local impact studies. They targeted migration and survival of large, hatchery-released stocks and ignored the many shallow-water habitat types typically favored by smaller subyearling migrants (Bottom et al. 2005). Moreover, until very recently, research tools were not available to identify the upriver sources of unmarked fish sampled in the estuary or to reconstruct population-specific patterns of estuarine migration, residency, or habitat use.

In 2002, we initiated a research program to address many of the data gaps identified in SARE (Bottom et al. 2005) where information was needed to support salmon recovery throughout the basin. To this end, we focused particularly on acquiring information about the habitat requirements of subyearling salmon with estuarine life histories. This report summarizes our results through 2006. The goal of our research was to determine historical and contemporary variations in juvenile salmon life history, habitat opportunity, and performance, and to determine whether restorative actions in the

Columbia River estuary are needed to insure salmon recovery. Our research primarily targeted Chinook salmon, which exhibits the greatest diversity in juvenile life history (Healey 1991; Wissmar and Simenstad 1998), and which is also considered the most estuarine-dependent of Pacific salmon species (Healey 1982). Based on the results and remaining uncertainties of the SARE analysis (Bottom et al. 2005), we addressed the following questions:

1. What are the spatial and temporal patterns of juvenile Chinook salmon abundance and life history in near-shore habitats along the estuarine tidal gradient, and are these correlated with physical variables?
2. Do upriver populations of Chinook salmon exhibit distinct habitat-use patterns or food-web linkages along the estuarine tidal gradient?
3.
 - a. Do Columbia River Chinook salmon rear in tidal wetlands?
 - b. If so, to what extent does their wetland use (i.e., abundance, seasonality, and residency) and performance (i.e., foraging success, growth) vary among different wetland types along the estuarine tidal gradient?
 - c. Are upriver source populations associated with distinct wetland habitats or habitat types?
4.
 - a. Have changes in historical habitat opportunity diminished the capacity of the estuary to support juvenile salmon and the diverse life histories of upriver populations?
 - b. Have these habitat changes altered food webs, with similar consequences to salmon?
 - c. Do contemporary patterns of estuary use by salmon support the hypothesis that, in the last century, juvenile life history diversity of Chinook salmon has declined?

This report synthesizes the results of 5 years of estuarine research. It summarizes progress to date toward answering each of the above questions and discusses the management and research implications for future salmon recovery. Detailed methods, results, and analyses for the many research activities briefly highlighted in this overview will be published separately. Additional descriptions of our research methods are available in Roegner et al. (2005). A current list of student theses, agency reports, and peer-reviewed publications resulting from this research is provided in the Appendix.

APPROACH

We implemented two complementary studies to address the above questions. In 2002, with support of the U.S. Army Corps of Engineers (USACE), we initiated a coarse-scale survey of selected shallow, near-shore habitats in the lower estuary region (Figure 1; Roegner et al. 2005). This project established a series of fixed stations to continuously measure physical variables (e.g., water depth, salinity, temperature, velocities, etc.) in the lower estuary (Baptista 2006). In addition, beach-seining sites were established to track abundances, life histories, stomach contents, and genetic composition of salmon along the lower estuary tidal gradient (questions 1 and 2).

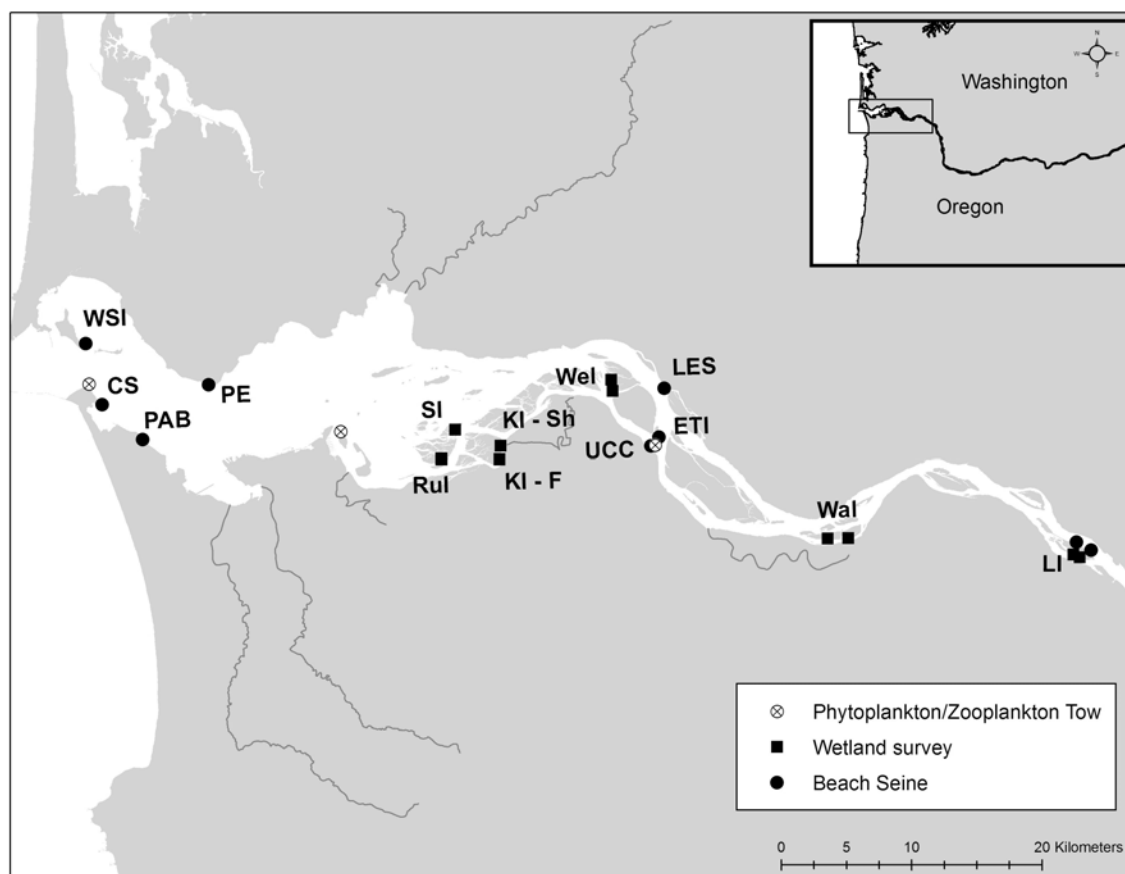


Figure 1. Sampling locations for the tidal gradient (beach seining), wetland habitat, and phytoplankton/zooplankton (stable isotope) surveys in the Columbia River estuary, 2002-06.

CS	Clatsop Spit	PAB	Point Adams Beach
PE	Point Elice	SI	Seal Island
Rul	Russian Island	KI-Sh/F	Karlson Island shrub/forested
Wel	Welch Island	UCC	Upper Clifton Channel
LES	Lower Elochoman Slough	ETI	East Tennesilahee Island
WAL	Wallace Island	LI	Lord Island

At a much finer (habitat) resolution, we also monitored fish and prey assemblages and surveyed vegetative communities within characteristic emergent, scrub/shrub, and forested wetland types distributed from rkm 35 to 101 (question 3). This research constituted the first systematic survey of juvenile salmon in Columbia River tidal wetlands, providing comparative data on salmon densities, performance, and upstream population sources among different wetland types. At a single indicator site—an emergent wetland at Russian Island (Cathlamet Bay)—we monitored fish and prey assemblages annually and conducted additional studies to estimate habitat-specific residence times, growth, and consumption of juvenile Chinook salmon. Sampling duration at the other wetland sites was limited to 2 or 3 years, allowing us to shift survey effort upriver to characterize a wider diversity of wetland types and geomorphic and hydrologic settings (Table 1). Detailed descriptions of sampling methods and results for the USACE monitoring project during the first 3 years of study were reported by Roegner et al. (2005).

Table 1. Years sampled (x) at each estuarine wetland site. Monthly samples were collected March-July or August during each survey year, including data on composition and abundance of fish (trap-net surveys), invertebrate prey resources (insect fallout trap and benthic core surveys), and salmon stomach contents. A pair of channels was sampled for fish and invertebrates at each wetland site. The two channels at Karlson Island are listed separately because wetland type and sampling duration differed at each location.

Site	Wetland type	rkm	2002	2003	2004	2005	2006
Russian Island	emergent	35	x	x	x	x	x
Seal Island	emergent	37	x	x			
Karlson Island	scrub/shrub	42	x	x	x		
Karlson Island	forested	42	x	x			
Welch Island	scrub/shrub	53			x	x	
Wallace Island	forested/scrub/shrub	77					x
Lord Island	forested/scrub/shrub	101					x

With support from the Bonneville Power Administration, we initiated a complementary study in 2003 to evaluate the potential effects of historical habitat change on estuarine food webs and their implications for juvenile salmon (question 4b).¹ The BPA study analyzed stable isotopes of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ to identify organic sources supporting subyearling Chinook salmon in the estuary and to reconstruct the migratory and habitat pathways of individuals with different juvenile life histories. The study identified isotopic signatures for major plant and prey resources in the estuary and compared these results with the signatures incorporated in salmon tissues. This was the first empirical study in the Columbia River estuary to examine directly the hypothesis that habitat changes since the predevelopment period have adversely affected salmonid food webs. The BPA study also allowed us to examine patterns of estuarine migration and habitat use by individual salmon based on the isotopic signatures of muscle and liver tissues, variations in salmon macroparasite communities, and otolith-derived estimates of salmon residence times in the lower estuary (question 2). Methods and results of the stable isotope and otolith analyses are detailed by Anderson (2006).

Together the USACE and BPA studies provided data needed to interpret historical changes in estuarine habitat opportunities (question 4a). We reconstructed historical and contemporary habitat composition and distribution in the lower estuary in a Geographical Information System and quantified changes since the first topographic (T-sheet) and bathymetric (H-sheet) surveys of the Columbia River estuary were completed during the late 19th and early 20th centuries (U.S. Coast and Geodetic Survey 1868 to 1901). These results refined and updated an earlier habitat-change analysis by Thomas (1983) and established analytical protocols for extending the analysis to the entire estuary (to Bonneville Dam).

In addition, we developed a 3-dimensional circulation model of the estuary to study the dynamics of salmon habitat opportunity under varying river flow and bathymetric conditions and to compare the system response to alternative habitat- and flow-management scenarios. Real-time estuarine circulation data collected in the lower estuary for the USACE monitoring project provided the information to develop and validate the 3-dimensional CORIE modeling system (Baptista 2006) used in the BPA study. The T-sheet and H-sheet data described above also improved the bathymetric baseline needed to support simulations of historical habitat conditions. The modeling system relies on two new circulation models (ELCIRC and SELFIE) that substantially improve the reliability of habitat-opportunity simulations compared with the previous results of a 2-dimensional model reported in SARE (Bottom et al. 2005). Details of the ELCIRC model are provided by Zhang et al. (2004) and Baptista et al. (2005), and details of the SELFIE model are reported in Zhang and Baptista (2008).

¹ BPA project 20031000n: Historic habitat opportunities and food-web linkages of juvenile salmon in the Columbia River estuary and their implications for managing river flows and restoring estuarine habitat.

RESULTS

Patterns of Abundance and Life History in Near-Shore Habitats

Abundance and Mean Size

From 2002 to 2006, we collected monthly beach-seining samples at the following seven sites in the Columbia River estuary: two in the marine zone near the estuary mouth (rkm 9.9-12.1); two within the tidal mixing zone below Tongue Point (rkm 19.8–22.0); and three in the vicinity of Tenasillahe Island (rkm 79.2–83.6), within the tidal freshwater zone (Figure 1). In 2006, we added four additional beach-seining sites to extend the tidal-gradient survey area upriver as far as rkm 101 and to provide supporting data for adjacent wetland surveys at Wallace and Lord Islands (described below).

In all years, we found Chinook salmon present in the estuary during all months of the year, whereas chum salmon occurred for a brief period in the spring (Figure 2). Seasonal patterns of Chinook salmon abundance were relatively consistent among years: abundance increased steadily from January, reached a peak in late spring and early summer, and declined rapidly after July. Salmon catches generally exhibited a longitudinal gradient with the highest catch per unit effort at tidal freshwater stations and the lowest values near the estuary mouth. Several factors may contribute to this pattern, including greater concentration of salmon (and increased sampling efficiencies) in the narrow freshwater sections of the estuary and cumulative losses from the estuary population through mortality and emigration.

In all years, mean sizes of juvenile Chinook salmon increased rapidly throughout the year at all estuary zones (Figure 3). Recently emerged fry appeared at all sites simultaneously in early spring, a pattern similar to the basin-wide dispersal of emergent fry reported in other Northwest rivers and estuaries (Healey 1991; Bottom et al. 2005). Fry migrants (< 60 mm) remained abundant in the estuary from January through April or May. By April, mean sizes of juvenile Chinook salmon increased along a spatial gradient from the tidal freshwater zone to the estuary mouth. This pattern likely reflects the increased growth of individuals during residency and migration through the estuary, as well as a continued arrival of smaller fish from upriver.

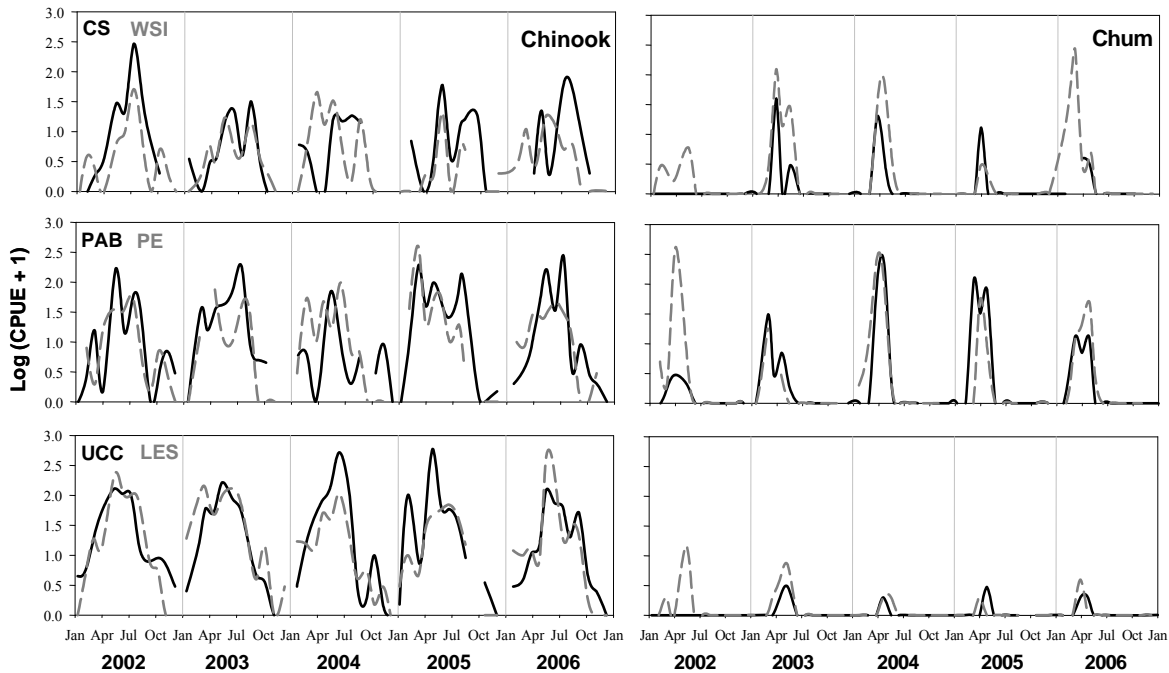


Figure 2. Smoothed curves of catch per unit effort for Chinook and chum salmon at beach-seining stations in the Columbia River estuary, 2002-2006. Stations grouped by habitat type are keyed as follows: marine, — CS (Clatsop Spit), --- WSI (West Sand Island); estuarine mixing, — PAB (Point Adams Beach) and --- PE (Point Elice); and tidal freshwater, — UCC (Upper Clifton Channel) and --- LES (Lower Elochoman Slough) areas.

Mean sizes of salmon often decreased or leveled off after April, particularly at tidal freshwater sites, and could indicate an increased rate of influx by slightly smaller fish during spring and early summer. For example, hatchery releases in 2003 and 2004 peaked during June, and the average size at release leveled off in May and June (CRDART 1995), a pattern which could influence the size decrease observed among fish sampled in the estuary (Figure 3). However, density-dependent interactions during the period of maximum salmon abundance also could have contributed to observed size trends in the estuary. For example, year-to-year seasonal decreases in the mean growth rate of wild Chinook salmon in southern Oregon's Sixes River estuary were attributed to food limitation as the population approached its mid-summer peak (Reimers 1973).

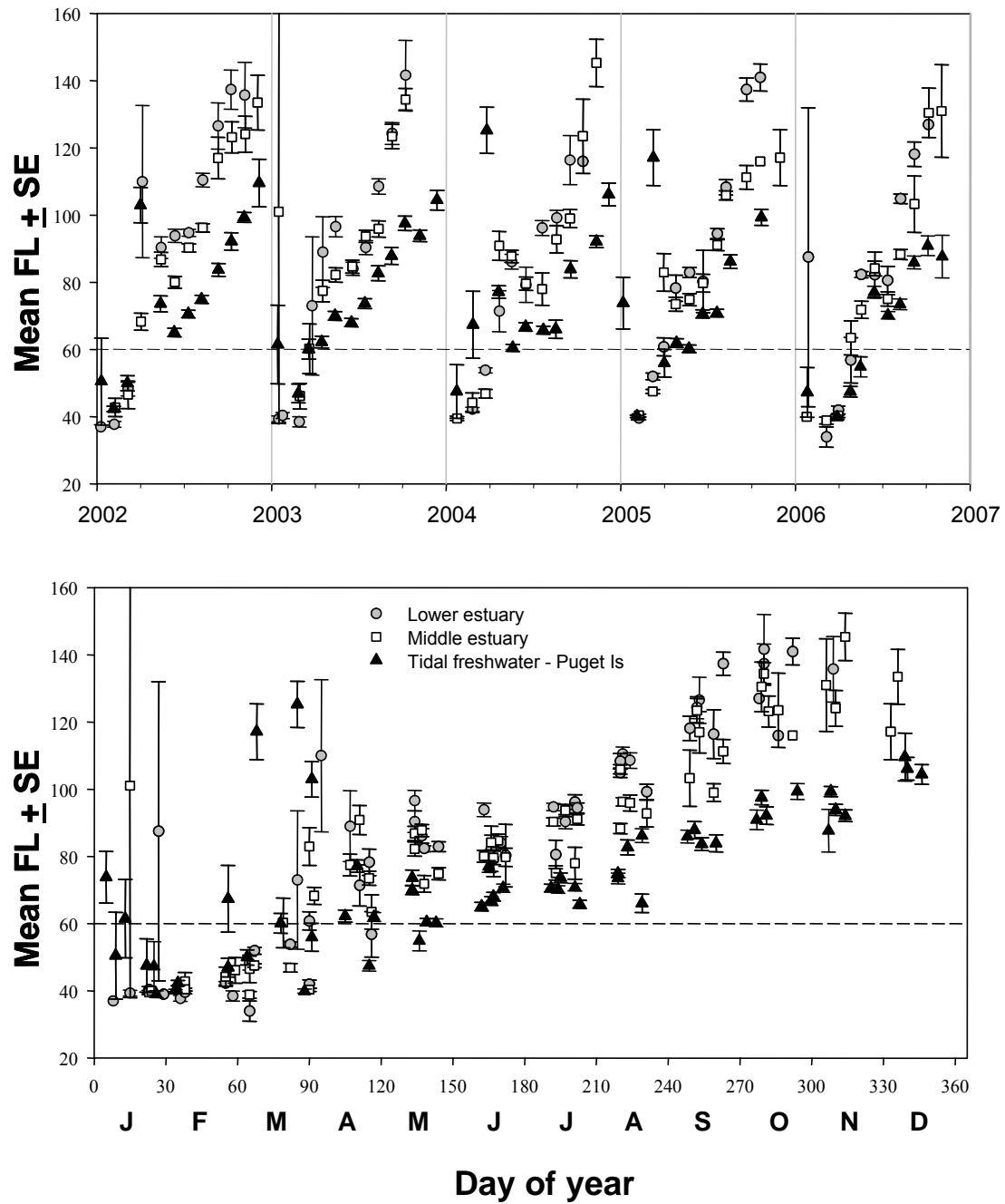


Figure 3. Mean sizes and standard error for juvenile Chinook salmon at beach-seining sites in the marine (○), estuarine mixing (□), and tidal freshwater (▲) zones for each year (upper graph) and for all years combined (lower graph), 2002-2006.

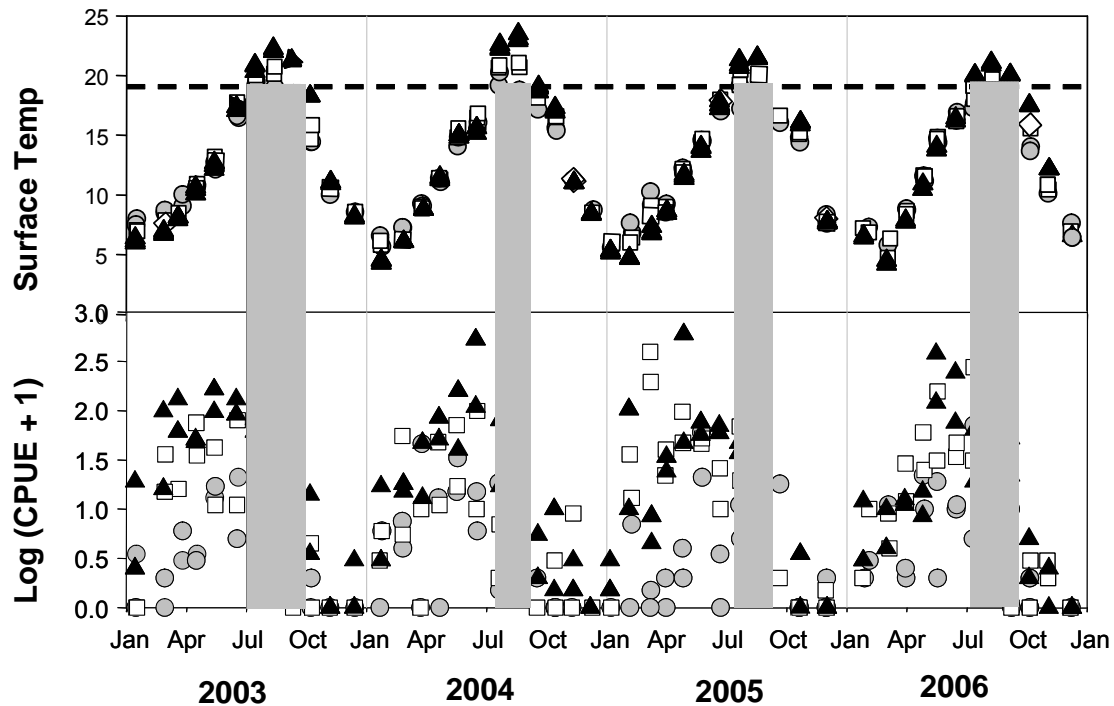


Figure 4. Mean surface water temperatures and Chinook salmon catch per unit effort at beach-seining sites in the marine (\circ), estuarine mixing (\square), and tidal freshwater (\blacktriangle) zones of the lower estuary, 2003-2006.

The rapid decline in Chinook salmon abundances each year after July generally coincided with high surface-water temperatures, particularly at sites located above the moderating effects of saline ocean water. Although conditions varied annually, temperatures at beach-seining sites in the tidal freshwater and mixing zone sites typically exceeded 19 or 20°C by July and remained above this threshold through August or September (Figure 4). These results suggest that estuarine rearing opportunities in shallow estuarine habitats may decline by mid summer, and fish may begin leaving the estuary or seeking deeper offshore habitats soon after salmon abundance has peaked and surface water temperatures have approached stressful levels. Increased mortality after the mid-summer peak also could be a factor in the observed population pattern, but we have not measured natural mortality trends in the estuary.

Estuarine Residency

We analyzed otolith chemistry to reconstruct the juvenile life histories and estuarine residency of individual Chinook salmon (e.g., Zimmerman 2005). Because the otolith technique measures an individual's first encounter with salt water (based on elevated Sr levels in the otolith), it does not account for residency periods within the long tidal freshwater zone of the Columbia River estuary. Nonetheless, many subyearling Chinook salmon remained for extended periods within the lower (salt-influenced) portion of the estuary. In 2004 for example, 41% of the otolith samples analyzed from Point Adams Beach (in the estuarine mixing zone) showed evidence of saltwater rearing prior to capture. Estuarine residency among these individuals averaged 73 d and ranged from 10 to 219 d.

We estimate that nearly half (46%) of these individuals entered the estuary at a size less than 60 mm, and 11% entered as recently emerged fry (< 40 mm). In contrast, previous estimates for Chinook salmon derived from marked hatchery groups yielded residency periods of about 1 week (Dawley et al. 1986). These results may have underestimated residency because values were derived from the first estuary recaptures of large batches of similarly marked hatchery fish. Previous estimates also may have been biased for individuals with short residence times, since large hatchery-fed fish may be least likely to rear in the estuary for additional periods before migrating to the ocean (Bottom et al. 2005). Despite significant effects of contemporary hatchery programs on stock composition, time of estuarine arrival, abundance, and mean length of juvenile salmon (Dawley et al. 1986; Bottom et al. 2005), our otolith results confirm that a significant proportion of the subyearling Chinook salmon population still lingers in the estuary for weeks or months before migrating to sea.

Habitat Use, Source Populations, and Food Webs along the Estuarine Tidal Gradient

Feeding and Growth

Measurements of stomach contents from samples collected at near-shore beach-seining sites in the lower estuary indicated that most juvenile Chinook salmon fed actively during their estuarine residency. In 2002–2006, monthly mean stomach fullness values by volume varied between 70.2 and 100% ($n = 1,554$ stomachs). Less than 1% ($n = 15$) of these stomachs were completely empty; only 1.8% ($n = 28$) of the stomachs were <10% full. In contrast, a much greater proportion of empty Chinook salmon stomachs (as high as 12%) was reported during a 1980-1981 survey of lower estuary fishes (Bottom et al. 1984).

Adult insects and epibenthic amphipods *Americorophium* spp. were the most important prey items of subyearling salmon at all lower-estuary sites in 2002-2005 (Figure 5). Whereas *A. salmonis* was more prevalent in samples from the tidal freshwater zone, *A. spinicorne* dominated the stomach contents of individuals collected in the

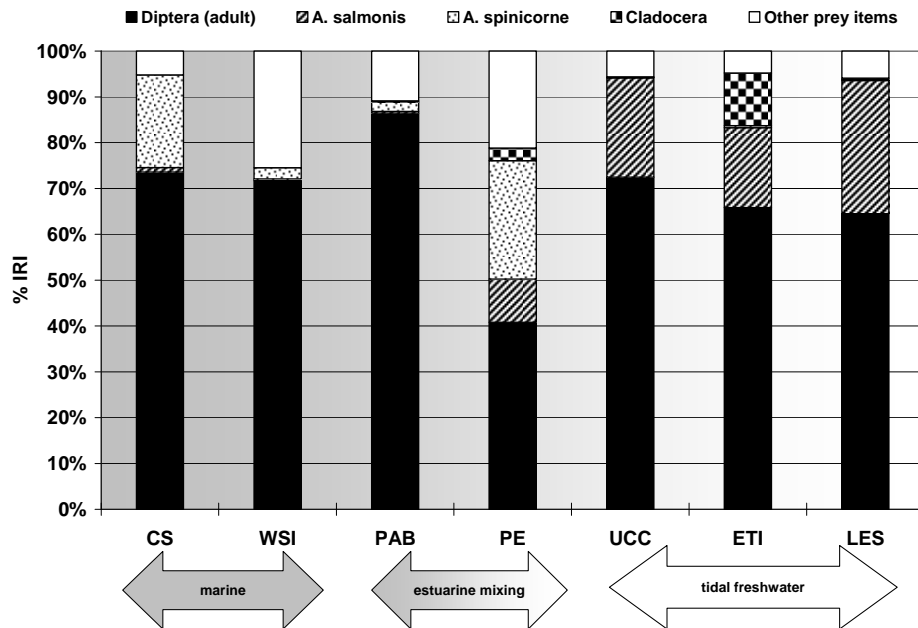


Figure 5. Major prey taxa consumed by juvenile Chinook salmon at seven beach-seining sites in the lower Columbia River estuary, 2002 to 2005. Prey taxa are ranked as a percent total of the Index of Relative Importance (IRI, Pinkas et al. 1971), which integrates frequency of occurrence, and percentage total biomass and numerical composition of each prey taxon.

estuarine mixing (Point Adams Beach and Point Ellice) and marine (Clatsop Spit and West Sand Island) zones. This feeding pattern was consistent with reports of a general decline in *A. salmonis* abundance toward the estuary mouth (Holton et al. 1984).

Studies during 1980-1981 similarly listed cladocerans (in the summer), *Americorophium* spp., and insects among the major prey taxa of subyearling Chinook salmon (e.g., Bottom et al. 1984; Bottom and Jones 1990). In contrast, our 2002-2005 survey more consistently ranked adult dipterans as the most important prey taxon at all lower estuary beach-seining sites. A recent study estimated that semi-aquatic dipterans and other marsh insects are nearly twice as energy-rich (kJ g^{-1}) as *Americorophium* spp. and other estuarine crustaceans (Gray 2005).

Growth rate estimates derived from daily growth increments on otoliths indicated that juvenile Chinook salmon directly benefit from foraging opportunities within the Columbia River estuary. During their estuarine residency, Chinook salmon grew on average approximately 0.5 mm d^{-1} (range $0.06\text{-}1.06 \text{ mm d}^{-1}$). This rate was comparable to growth estimates reported for juvenile Chinook salmon in other Northwest estuaries (Healey 1991).

Genetic Stock Groups

To determine whether the patterns of estuary use and performance vary among source populations, we used microsatellite DNA markers to estimate the stock origins of Chinook salmon collected in the estuary. The analysis used 13 loci and standardized baseline data from 36 Columbia Basin populations (the GAPS database; Seeb et al. 2007). Estimates of proportional stock compositions in samples and the stock origins of individual fish were made using the software GMA (Kalinowski 2003). In initial testing, we identified the following six genetic stock groups for estimating the origins of unknown individuals:

Interior Spring
Interior Summer/Fall
Spring Creek Fall
Upper Willamette Spring
Western Cascade Fall
Western Cascade Spring

Of the 1,004 samples we analyzed from estuary beach seine collections in 2002-2004, approximately 90% were fall Chinook from the Lower Columbia River ESU (Spring Creek and Western Cascades Fall groups). However, small proportions of spring run

Chinook from the Lower Columbia River (3%) and Upper Willamette River (1%) ESUs and summer- and fall-run fish from the interior Columbia Basin (6%) also were sampled. Although spring-run fish from the interior basin also were estimated to comprise a very small proportion of the catches (<1%), no individuals were assigned to that stock group with high probability. Nonetheless these results indicate that salmon collections throughout the estuary were composed of fish from a diversity of ESUs (Figure 6).

Genetic Stock Assignments

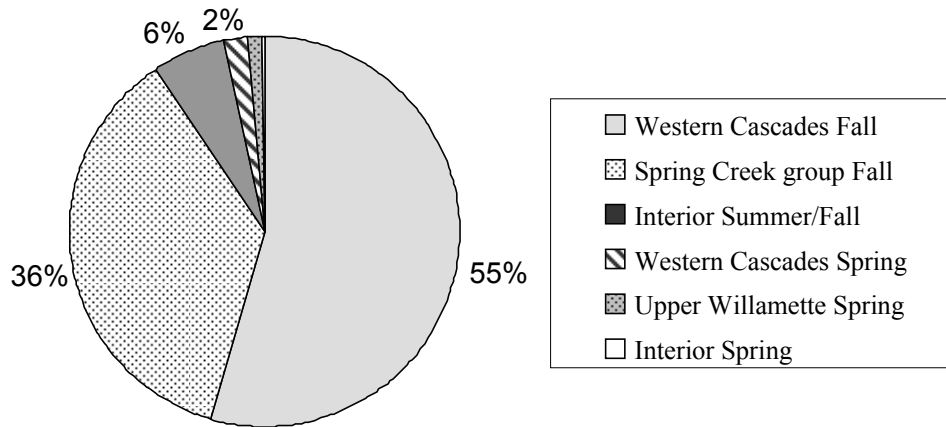


Figure 6. Estimated proportions of 6 major Chinook salmon stock groups from seven beach-seining sites in the lower Columbia River estuary, 2002-2004 (n = 1,004).

While multiple ESUs were represented during all months, stock groups exhibited distinct spatial and temporal abundance patterns in 2002-2004 (Figure 7). The Spring Creek Falls group peaked in the estuary in May and declined thereafter. Western Cascade Falls migrants were present throughout the year but reached their greatest abundance in July after the Spring Creek Falls group had declined. This general temporal sequence—a peak in Spring Creek Falls abundance followed by a peak in Western Cascade Falls—was consistent among years. Among minor stock groups, the Interior Summer/Fall run group gradually increased and decreased on either side of a July peak, while the few Upper Willamette Springs fish occurred between January and July only.

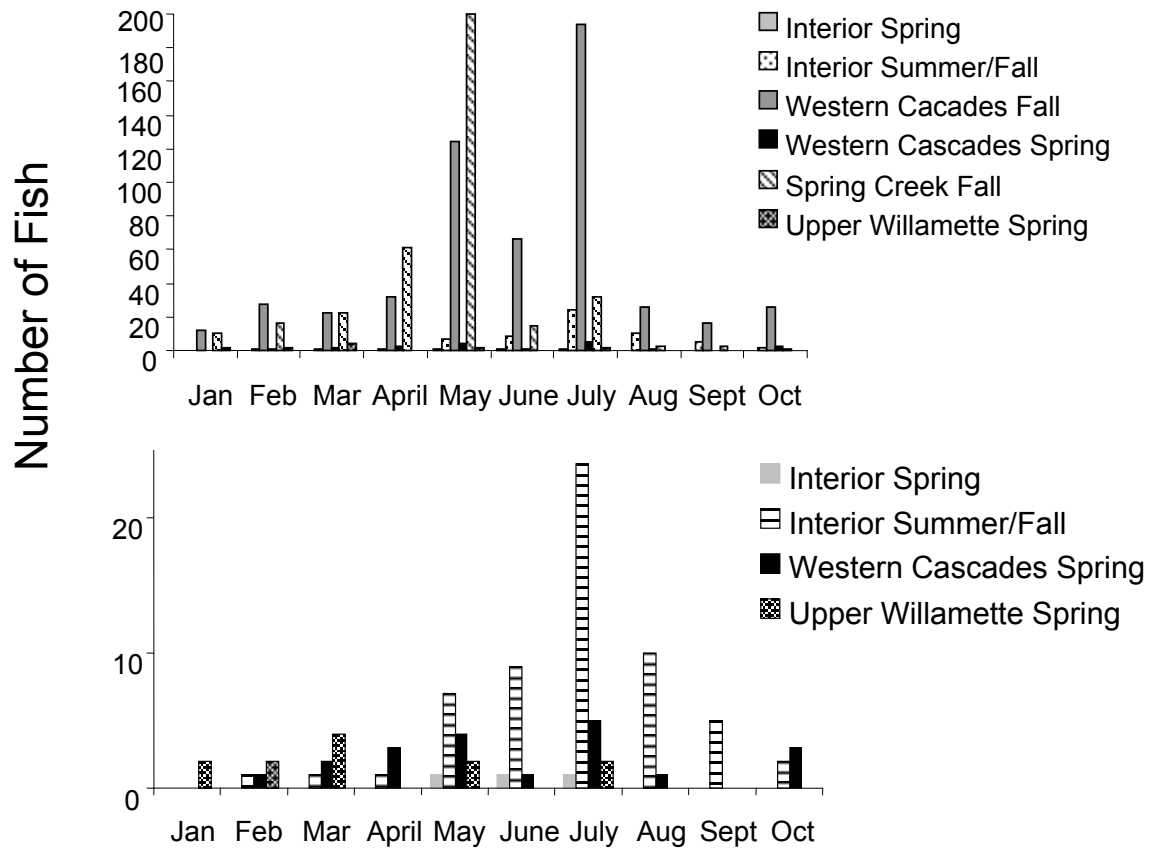


Figure 7. Genetic assignments for juvenile Chinook salmon sampled with the beach seine for all sites and years combined in 2002-2004 ($n = 1,004$). Lower panel depicts minor stock groups only.

Parasites, Organic Matter Sources, and Habitat-Use Patterns

We examined the macroparasite communities of 828 Chinook salmon sampled with the beach seine in 2002-2004 as a potential indicator of salmon habitat use and life history patterns in the estuary. A total of 457 salmon or 55% of all samples were infected with at least one parasite species. Three different acanthocephalan species (*Echinorhynchus* sp., *E. lageniformis*, and *Neoechinorhynchus* sp.) and three nematode species (*Hysterothylacium* sp., an unidentified intestinal nematode, and *Salvelinema* sp.) were recovered from salmon intestines and swim bladders.

In all three years, samples collected at Lower Elochoman Slough showed evidence of a turnover in the parasite community in June, particularly among acanthocephalan species, which could represent a shift in the stock composition and associated habitat-use and feeding histories among individuals at the site. In 2003, for example, prevalence of acanthocephalans in juvenile Chinook salmon declined substantially during June and was absent for months thereafter (Figure 8B).

Since acanthocephalan life spans extend for approximately one year, the abrupt decline suggests that infected fish had left the area and were replaced by individuals with different parasite loads and food habits. The parasite turnover each year at this site also coincided with the temporal shift in stock composition at Lower Elochoman Slough, as abundance of the Spring Creek Fall group declined substantially while the Western Cascade Falls and Interior Summer/Fall groups increased or maintained their abundance after June (Figures 7, 8A).

Stable isotope analyses of organic carbon sources for individual salmon sampled at Lower Elochoman Slough also indicated a temporal change in primary food sources during the summer (Figure 8C), including increased contributions from aquatic plant, benthic algae, and benthic diatom sources in June. Interpretation of stock-specific patterns of estuarine habitat use will require further comparisons of the juvenile life history, organic matter sources, genetics, and parasites for individual fish. For example, although lack of a temporal pattern in the salmon parasite assemblages at Point Adams Beach could be explained by increased mixing of stocks near the estuary mouth, the genetic stock groups at Point Adams Beach exhibited seasonal patterns similar to the trends recorded at Lower Elochoman Slough.

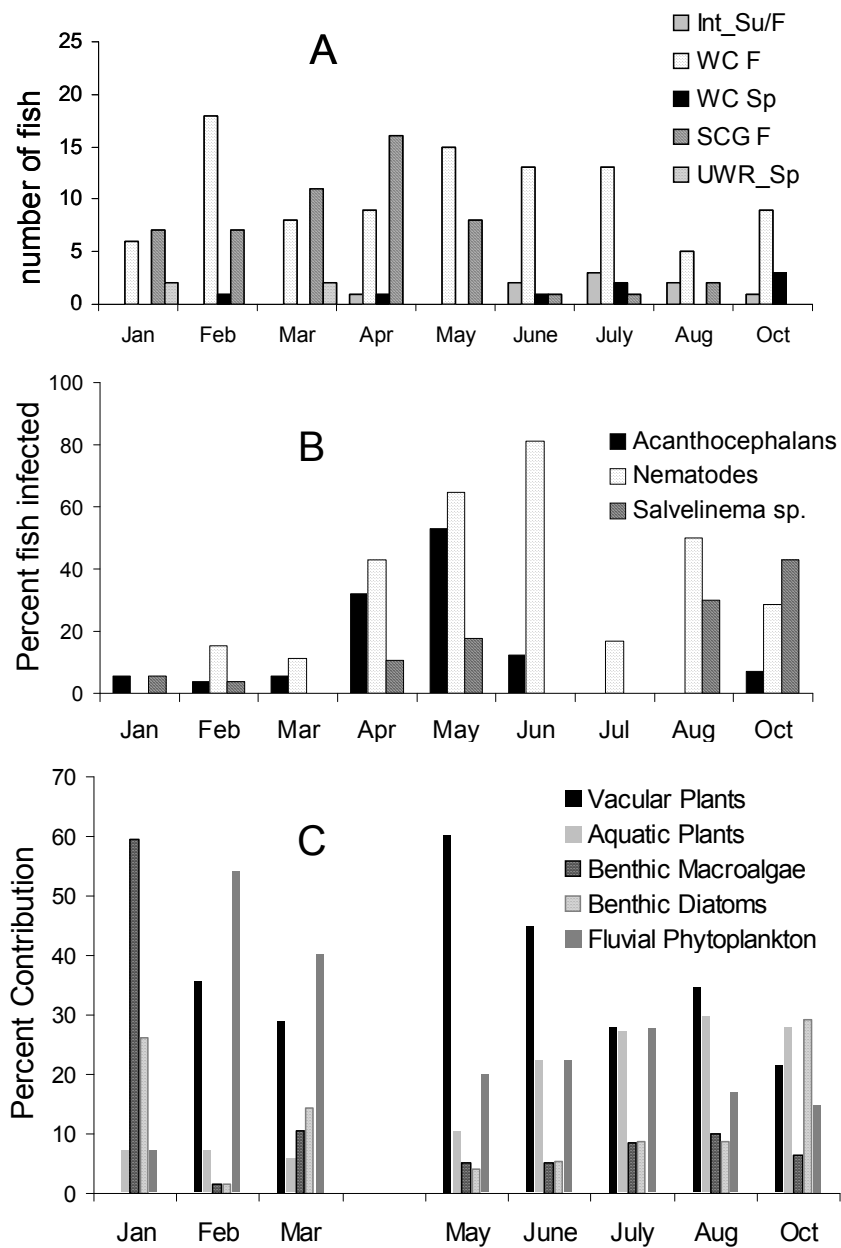


Figure 8. Monthly genetic stock group assignments (A), intestinal parasite composition (B), and organic matter sources (C) for fish sampled at Lower Elochoman Slough in 2003.

From stable isotope analyses of juvenile salmon tissues, we identified 13 types of estuarine rearing strategy as defined by food-web linkages (Table 3). Common sequences of habitat use and movement included transitions from fluvial and benthic food webs to marsh food webs, and from marsh food webs to fluvial and marine food webs. The rarest life histories, in terms of membership of the population, were composed of individuals that showed no sign of hatchery rearing and relied heavily on marsh production in the estuary. Most groups displayed diverse habitat associations, using freshwater wetland, fluvial, estuarine wetland, and marine food web resources. Interaction with marsh food webs was substantial for all subyearling Chinook salmon. The average time individual fish interacted with wetland-based food webs was estimated on the order of weeks to months throughout the estuarine habitat complex. We found no indication that food web use was linked to stock of origin; however, sample sizes generally were too low for this type of comparison.

Table 3. Summary of cluster types, and the percent membership, average length (mm), location and month of capture, and associated mixing model results (muscle and liver tissues) for each cluster. Muscle reflects long- term dietary sources on the order of weeks, whereas liver reflects short-term diet on the order of days. The origin (if known), predominant signature of muscle and liver, and relative marsh residence times (high, medium, or low) for each cluster is also shown.

Cluster	Member- ship (%)	Length (mm)	Area	Month	Origin	Muscle	Liver	Marsh Residency
1	0.9	80	Lower	Jul		Marsh	Marsh	High
2	0.9	66	Mid	May		Benthic	Marsh	High
3	0.9	87	Upper	Oct		Marsh	Fluvial	High
4	1.9	99	Lower	Jul	Hatchery	Hatchery	Marine	Low
5	1.9	82	Lower	Jul		Benthic	Mixed	Med
6	1.9	85	Lower	Jul	Hatchery	Marsh	Fluvial & Marine	High
7	5.7	80	Mid	May	Hatchery	Hatchery	Mixed	Low
8	5.7	72	Upper-Mid	Jun	Hatchery	Fluvial	Fluvial	Med
9	5.7	77	Upper-Mid	Jun	Hatchery	Fluvial	Marsh	High
10	8.5	78	Upper-Mid	Aug		Fluvial	Marsh	High
11	18.9	71	Mid-Lower	Jun	Hatchery	Hatchery	Benthic	Med
12	22.6	77	Mid-Lower	Jun	Hatchery	Hatchery	Marine	Low
13	24.5	67	Upper-Mid	May	Hatchery	Fluvial	Marsh	High

Salmon Habitat Use, Performance, and Source Populations within Wetland Habitats

Salmon Densities and Size Classes

From March through July in 2002-2006, we surveyed a series of tidal wetlands to compare salmonid use and performance among characteristic wetland types. Our results indicated that subyearling Chinook salmon rear in tidal wetlands of all types throughout the lower 100 km of the estuary (Figure 9). Although other species, such as threespine stickleback *Gasterosteus aculeatus*, often dominated catches at particular sites, juvenile Chinook salmon nonetheless were among the top few species at each wetland site from

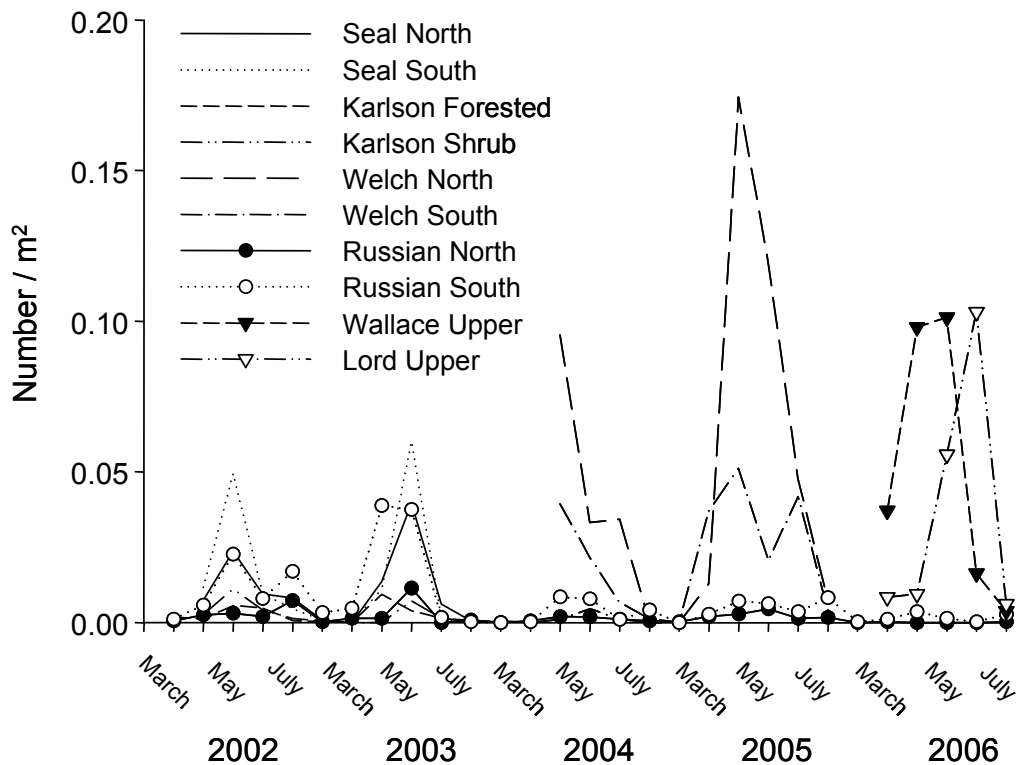


Figure 9. Estimated densities of subyearling Chinook salmon within wetland study channels chosen at each island survey site. Salmon abundances were adjusted by the average sampling efficiency for each fyke trap net (based on release and recapture of marked salmon above each site). To compare abundances among sites, adjusted counts are expressed as densities based on GIS estimates of the total channel area sampled above each trap net.

March through July. Seasonal peak densities of salmon ranged from <0.01 fish m^{-2} at Karlson (scrub/shrub and forested) and Seal Island south channels to 0.17 fish m^{-2} at Welch Island north channel.

Peak spring densities of juvenile salmon were particularly high at scrub/shrub and forested sites in the upper 50 km of our study area, including the tidal freshwater wetlands at Welch Island, Wallace Island, and Lord Island. Most seasonal peak densities for Chinook salmon in the Columbia River wetlands are within the range of values (0.02 - 0.11 fish m^{-2}) that has been reported for natural and restored marshes at Salmon River estuary on the central Oregon coast (Bottom et al. 2005; Cornwell et al. 2001). Salmon densities at all Columbia River sites fell to low levels by July, coincident with high water temperatures in shallow wetlands that approached or exceeded $19^{\circ}C$ during summer.

Columbia River wetlands were used primarily by smaller size classes of Chinook salmon. Many fry (~ 40 mm) entered wetland habitats soon after emergence in the spring. In contrast to the size ranges represented at lower estuary beach-seining sites (Figure 3), few individuals in any of the wetland channels exceeded 90 mm (Figure 10). The size

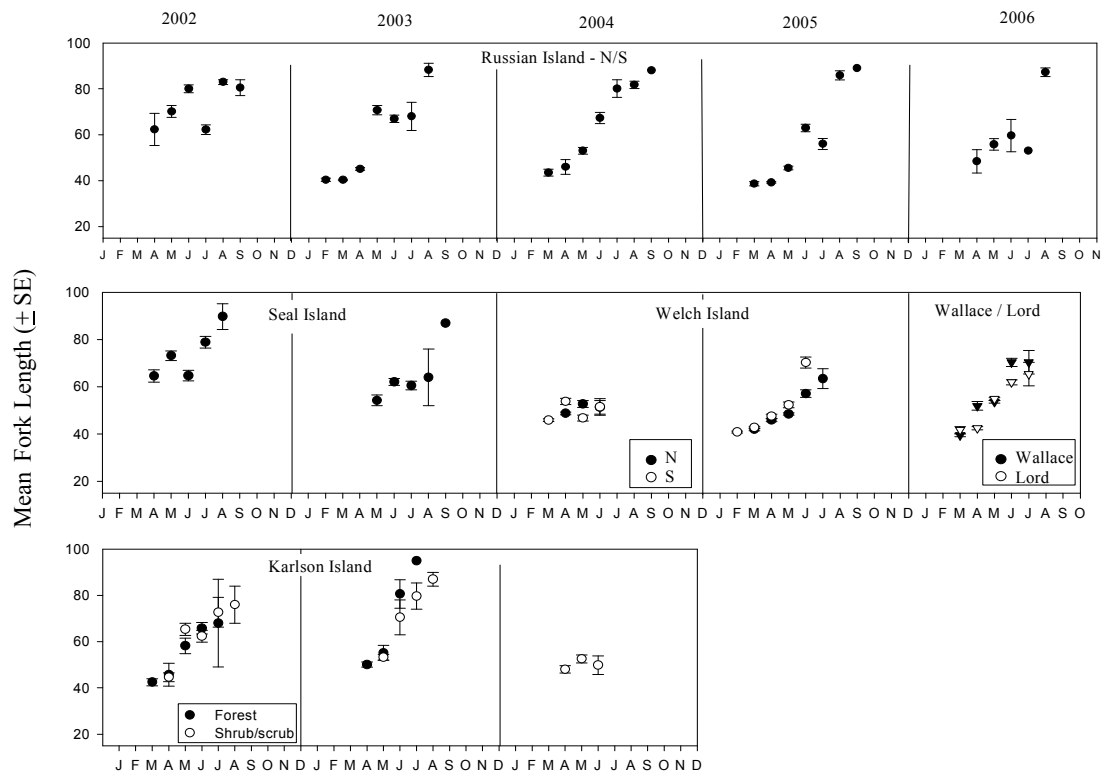


Figure 10. Monthly length frequencies (mm) of juvenile Chinook salmon collected in wetland channels at Russian Island (rkm 35) in 2002-06; Seal Island (rkm 37) in 2002-2003; Karlson Island forested and shrub sites (rkm 42) in 2002-2004, Welch Island (rkm 53) in 2004-2005, and Wallace and Lord Islands (rkm 77 and 101) in 2006.

range was smallest for tidal freshwater wetlands above rkm 50 (i.e., Welch, Wallace, and Lord Islands), where salmon rarely exceeded 70 mm at the end of the rearing season. These results were consistent with the hypothesis that estuarine-resident salmon with subyearling life histories may depend on rearing opportunities in shallow, low-velocity wetlands (Bottom et al. 2005).

Residency within Wetland Habitats

We studied the residency of juvenile salmon at two small study areas within a large distributary channel that bisects the Russian Island emergent wetland complex in Cathlamet Bay (Figure 1). In 2006 we marked and released 918 juvenile Chinook salmon within two small sections of the channel, and recaptured a total of 224 (24%) individuals over the next five weeks (Figure 11). Based on the cumulative recapture curve, we estimated median residency for individuals within the two study areas was approximately 5 d. An additional 14% of the marked population remained for more than two weeks, and maximum recorded residency was 34 d. These represent minimum values since residence times may be substantially underestimated using conventional mark/recapture methods: some individuals could have arrived at the site many days prior to initial marking, others may have remained somewhere within the expansive Russian

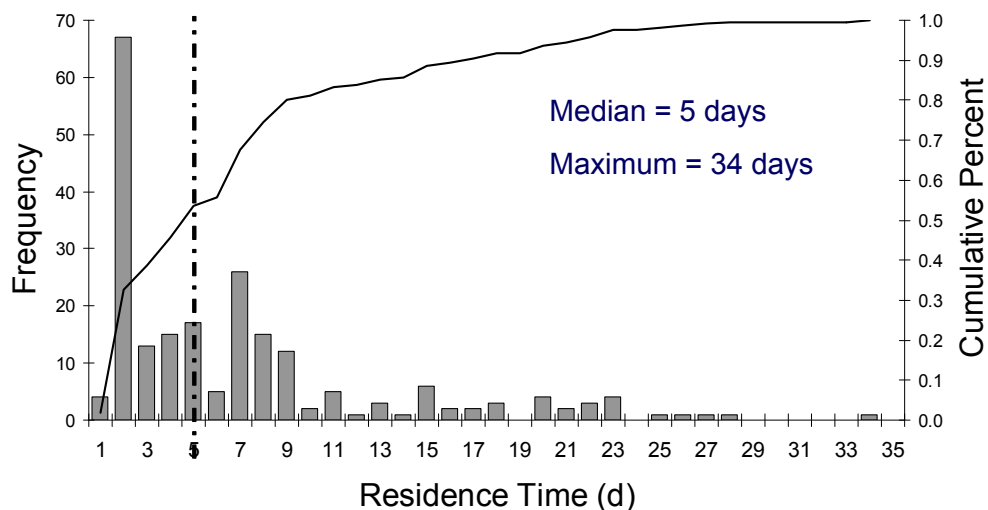


Figure 11. Days elapsed between release ($n = 918$) and cumulative recaptures ($n = 224$) of marked juvenile Chinook salmon in a Russian Island marsh channel in April 2006. Median residency was estimated as approximately 5 d based on the time elapsed when 50% of all recaptures were tallied.

Island marsh complex beyond our limited recapture area, and others could have returned to the site long after the experiment was terminated. In Oregon's Salmon River estuary for example, a remote PIT detector recorded intermittent use of a small secondary channel by some individual Chinook salmon, including one fish that returned to the site 109 d after its initial detection (Hering and Bottom 2006). Thus, daily or less frequent sampling at a few locales may significantly underestimate the frequency and duration of habitat use by individual fish. The Russian Island results demonstrated that, at a minimum, many Columbia River Chinook salmon returned to the same site for days or weeks despite having to vacate the channel twice daily at low tide.

Prey Composition, Daily Ration, and Growth

Prey availability studies and salmon diet information indicated that tidal wetlands are a major source of food for juvenile Chinook salmon both within and outside wetland habitats. Within the wetlands surveyed, the diets of subyearling salmon were dominated by chironomid insects, particularly emerging adults (Figure 12). Chironomids also were

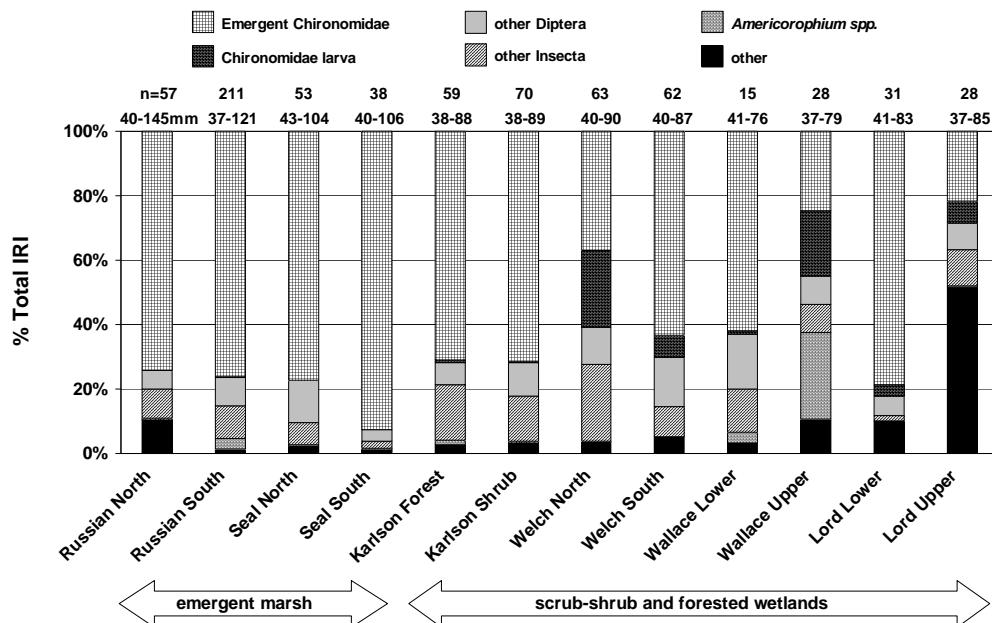


Figure 12. Major prey taxa consumed by juvenile Chinook salmon at each wetland type throughout each survey period, 2002-2006. Prey taxa are ranked as a percent total of the Index of Relative Importance (IRI; Pinkas et al. 1971), which integrates frequency of occurrence, percent total biomass, and numerical composition of each prey taxon. Sample size and range in fish fork length are listed for each site.

among the most abundant prey taxa available to salmon within each wetland type as indicated by samples collected in the insect fallout traps (Figure 13).

Other principal prey taxa for salmon included epibenthic amphipods (predominantly *Americorophium* spp.), and a variety of additional insect taxa; the “other” category included other gammarid amphipods such as *Eogammarus* spp., mysids, and the cladocerans, *Bosmina* spp. Diets of Chinook salmon from diverse wetland habitat types (Figure 12) and along the estuary tidal gradient (Figure 5) indicate that chironomids and other insects produced in emergent wetlands and possibly other shallow habitats benefit salmon throughout the estuary, including larger size classes that do not typically reside within wetland channels. The estuary-wide influence of wetlands is further indicated by the many food webs based on marsh-derived plant sources with which juvenile salmon interact (Figure 9C).

We conducted two diel consumption studies (19-20 April 2005 and 1-2 June 2006) to determine feeding patterns and estimate daily consumption rates for juvenile Chinook salmon within the Russian Island marsh. In these studies, we sampled five Chinook salmon stomachs at approximately 3-h intervals during a 30-h period.

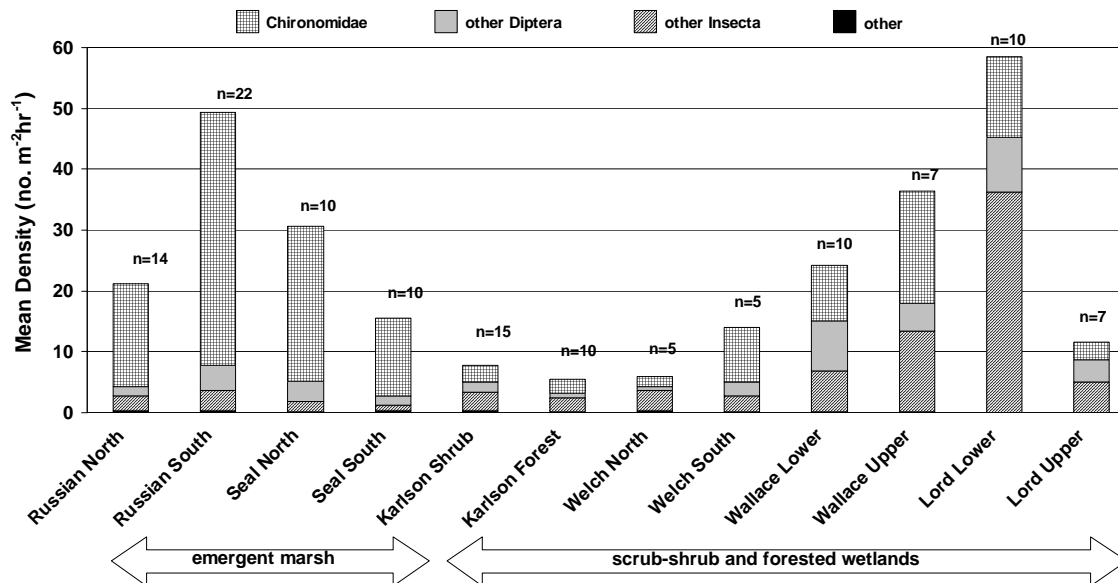


Figure 13. Mean density and composition of insects and other invertebrates sampled per hour of insect fallout trap deployment at each wetland site in May 2002-2006. Sample size is listed for each sampling site.

Results indicated that subyearling Chinook salmon directly benefit from residency in wetland habitats. We observed only one empty stomach among all fish analyzed during the two studies. Mean daily ration estimates at Russian Island marsh ranged from 11.3% body weight for 50-69 mm salmon in 2005 to 19.3% for 53-99 mm salmon in 2006. Consumption of emergent marsh-produced prey, in turn, supported growth by juvenile Chinook salmon. From recaptures of marked individuals during the 2006 residency study, we estimated that the average specific growth rate for Chinook salmon within the Russian Island wetland was 0.67 mm d^{-1} ($\text{SD} = 0.46$; $R = -0.83 - 2.1 \text{ mm d}^{-1}$). This result was very similar to independent estimates (0.5 mm d^{-1}) described above (section 2, Feeding and Growth) from otolith increment analysis of salmon collected in the estuarine mixing zone (Point Adams Beach).

Genetic Stock Groups

Wetland sites of all types directly supported a diversity of genetic stock groups. All groups identified at estuary beach-seining sites (Figure 6) also were represented in wetland channel habitats except for the Upper Willamette River Spring group (Figure 14). Most salmon vacated wetland channels by July or August. The Spring Creek Fall group declined through the spring and summer, similar to the trend observed at mainstem beach-seining sites (Figure 8A). Results to date suggest that wetland use among genetic stock groups may vary along the estuarine tidal gradient, including a somewhat smaller contribution by the Spring Creek Fall group at upper (i.e., Lord and Wallace Islands) relative to lower wetland (i.e., Karlson, Russian and Seal Islands) sites. Verification of spatial patterns of wetland habitat use among genetic stock groups will require additional sampling along the entire estuarine tidal gradient (to Bonneville Dam).

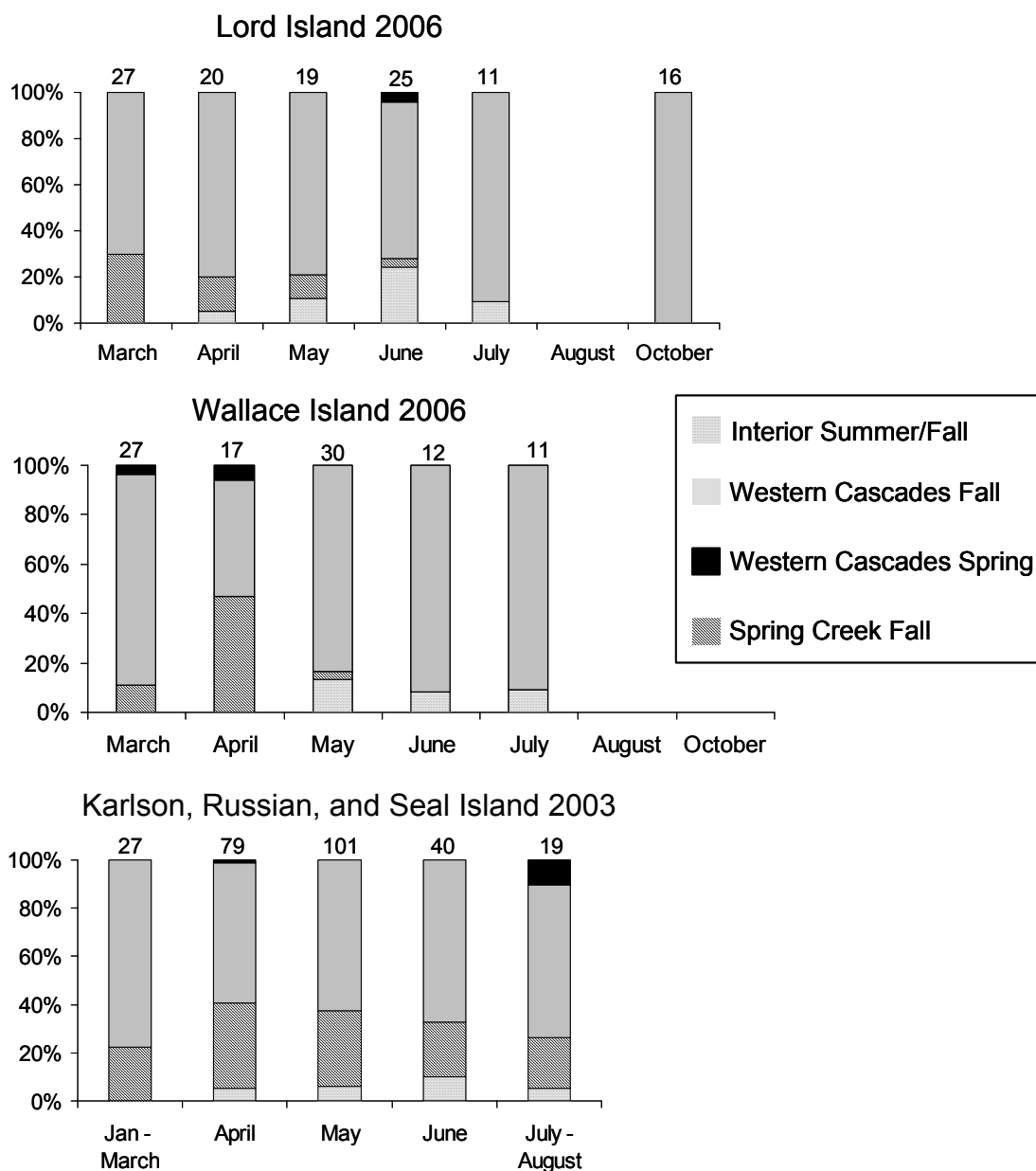
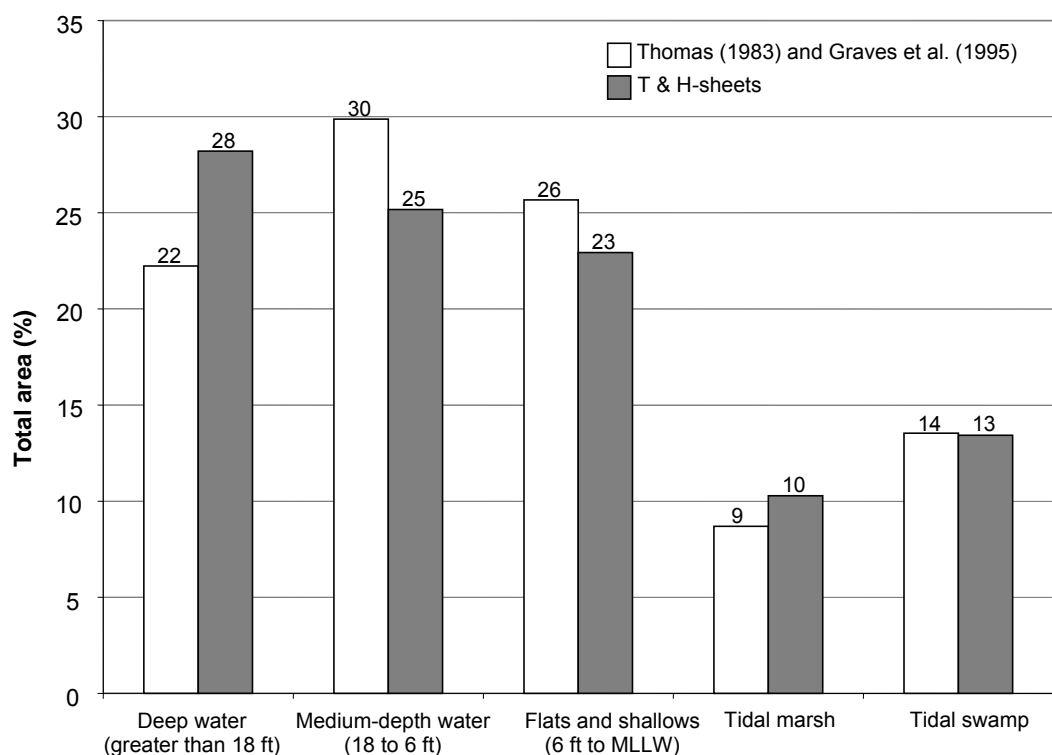


Figure 14. Juvenile Chinook salmon stock composition at Karlson, Russian, and Seal Island wetlands in 2003 and at Wallace and Lord Island wetlands in 2006. Abbreviations: WC-Western Cascades; SCG-Spring Creek Group; Su-summer; F-fall; Sp-spring.

Historical Changes in Salmon Habitat Opportunity, Food Webs, and Life Histories

Habitat Distribution

We digitized late 19th and early 20th century topographic (T-sheets) and hydrographic (H-sheets) survey data (U.S. Coast and Geodetic Survey maps dated 1868 to 1901) and classified historical habitat distributions in the lower Columbia River estuary (rkm 0–75) in a Geographical Information System (GIS). The higher-resolution T-sheets and H-sheets and our digital methodology improved the detail and accuracy of historical land cover and bathymetric habitat classes for the lower estuary compared with those originally reported by Thomas (1983) and Graves et al. (1995). Digitized historical data indicated slightly higher proportions of deep-water and tidal marsh habitats and somewhat lower proportions of medium-depth water, flats, and shallows than were previously reported (Figure 15).



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Figure 15. Lower estuary habitat areas derived from GIS analysis of historical T-sheets and H-sheets and those previously derived from nautical charts (Thomas 1983; Graves et al. 1995).

Estimated habitat changes since the time of historical surveys remain preliminary because we lack recent bathymetric data for shallows, flats, and many distributary channels, and tidal elevations during the Landsat data collection are unknown. Nonetheless, estimates derived from available Landsat satellite imagery suggest that total surface area of all wetland types within the lower Columbia River estuary has declined substantially since the late 19th and early 20th centuries (Figure 16). The largest estimated losses have occurred in scrub/shrub and forested wetland types, which have declined approximately 55 and 58%, respectively. We estimate that the total area of all marsh types combined (i.e., excluding the area of tidal flats) has decreased from approximately 155 to 75 km², a reduction of slightly more than 50%.

Loss of forested wetlands has been particularly high in the upper portion of the study area above Cathlamet Bay. The total area of emergent (tidal marsh) wetland types has declined by a smaller percentage, in part because marsh area has increased locally among many island habitats in Cathlamet Bay. Areas of shoaling in the vicinity of Cathlamet Bay also account for much of the increase in tidal flat area of the lower estuary. GIS mapping of historical and contemporary wetlands indicated that much of the shoreline marsh vegetation and associated dendritic channel networks have been removed from the lower estuary by diking and filling, substantially reducing the availability of peripheral wetland habitat to juvenile salmon.

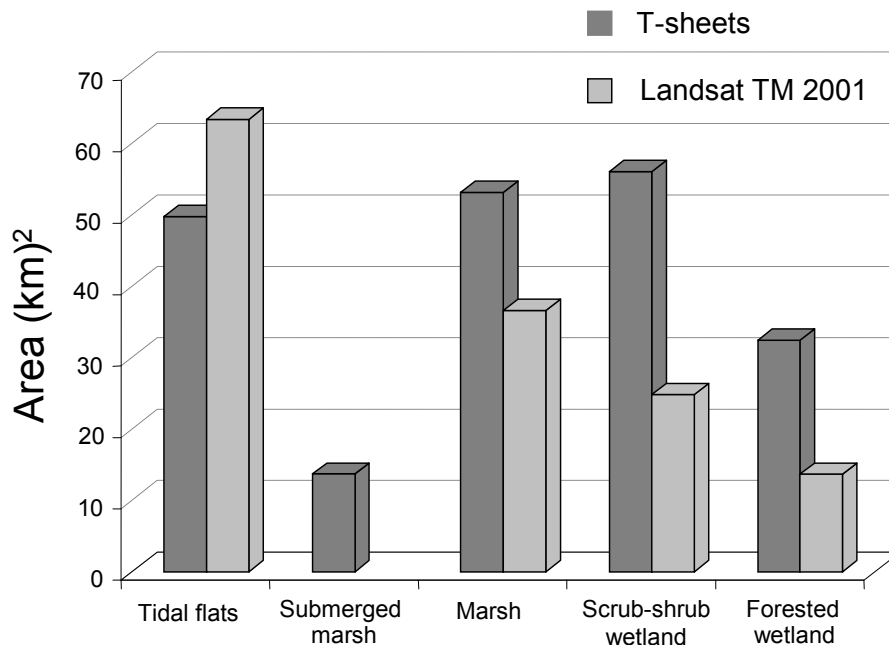


Figure 16. Estimated habitat areas and distributions derived from historical (T-sheets) and contemporary (Landsat TM 2001) surveys of the lower Columbia River estuary.

Habitat-Opportunity Dynamics

We used simulation modeling to examine the effects of bathymetric and hydrological change on salmon habitat opportunity, defined as the availability of shallow-water (10 cm to 2.0 m) habitats preferred by subyearling salmon (Bottom et al. 2005). The model contrasted habitat opportunity ($h \times m^2$ wetted area) in various regions of the lower estuary among the following management scenarios:

- 1) Predevelopment (1880) bathymetry and flow
- 2) Predevelopment bathymetry and flow with modern dikes introduced in the Brownsmead area (near rkm 50)
- 3) Predevelopment flow with modern bathymetry
- 4) Modern (2004) flow with predevelopment bathymetry
- 5) Modern flow with modern bathymetry

Simulation results suggest that flow regulation and bathymetric changes (i.e., diking and navigational development) have fundamentally altered the dynamics of river/floodplain interactions, eliminating considerable habitat opportunity in the uppermost tidal freshwater region of the lower estuary (Figure 17).

For example, in the predevelopment flow and bathymetry scenario, simulated habitat opportunity in this region showed a linear increase with river flow (Figure 17). On the other hand, habitat opportunity using modern bathymetry remained stable at relatively low levels throughout a wide range of flow conditions, reflecting the effects of peripheral dikes on floodplain areas. These results reinforced the earlier findings of Kulkala and Jay (2003a,b) who demonstrated that diking throughout the Skamokawa (rkm 50) to Beaver (rkm 90) region prevents inundation of the historical floodplain for a wide range of river flows.

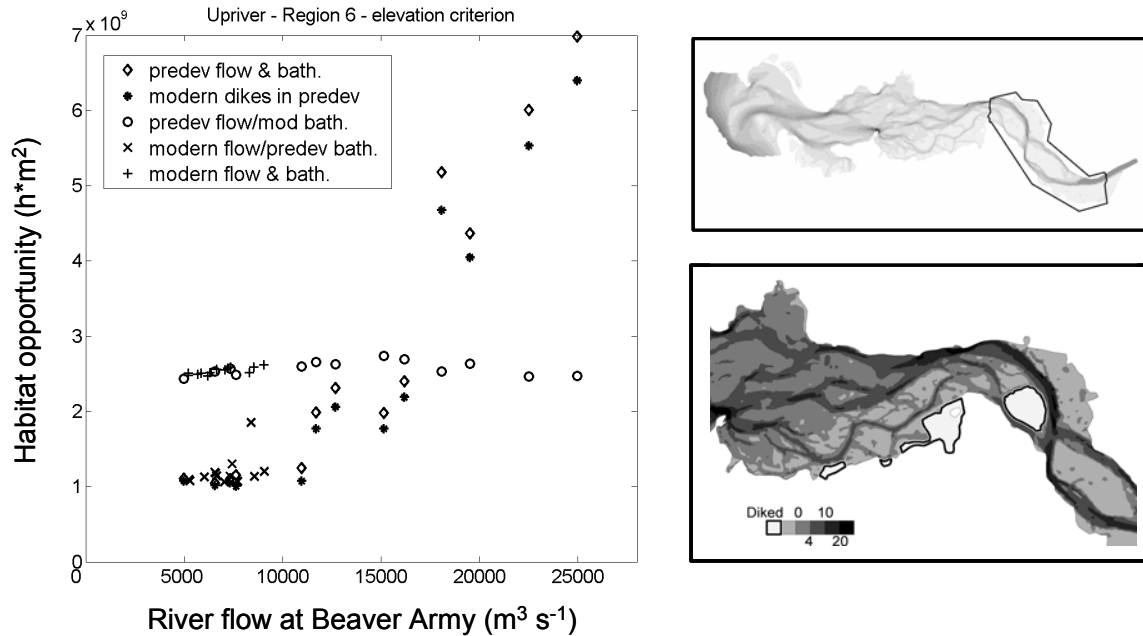


Figure 17. Weekly habitat opportunity in the uppermost region of the lower Columbia River estuary plotted against river flow for various modern and predevelopment scenarios (see text description). The modeling region is mapped in the upper right. The lower right figure outlines the dikes that were superimposed on the predevelopment bathymetry.

Simulation results have important implications for habitat restoration in the tidal freshwater regions of the estuary. For example, superimposing modern dikes in areas of Cathlamet Bay and Tennesillahe Island onto the predevelopment bathymetry reduced habitat opportunity for salmon (Figure 17; modern dikes in predev). However, this particular change did not alter the underlying linear response to increasing river flows. In contrast, the modern (regulated) flow regime has eliminated altogether the higher flow conditions that historically would have allowed salmonids to access much of the floodplain habitat (Figure 17; modern flow/predev bath).

These results illustrated the importance of hydrology to habitat function within this estuarine region, where the efficacy of dike removal or other habitat restoration projects also will depend on the underlying flow-management regime. Ultimately, restoring habitat access to juvenile salmon in the extensive tidal freshwater reaches of the estuary will require re-establishing river/floodplain connections through some combination of flow and habitat restoration (e.g., dike removal, setbacks, etc.). To better understand these effects, finer scale modeling will be needed to examine restoration alternatives for site-specific bathymetric and topographic conditions and selected flow-management scenarios.

Estuarine Food Webs

Loss of wetland habitat and reduced interaction with the tidal floodplain have not only reduced rearing opportunities for juvenile salmon, but may have eliminated an important carbon source for salmonid food webs. Sherwood et al. (1990) estimated that wetland losses eliminated approximately 15,800 metric tons of carbon per year or 84% of the macrodetritus that historically supported estuarine food webs. At the same time, enhanced phytoplankton production, which occurs in the reservoirs behind mainstem dams, increased the amount of microdetritus delivered from upriver sources by approximately 31,000 t C year⁻¹ (Sherwood et al. 1990). Fluvial phytoplankton now accounts for approximately 58% of the carbon available in the estuary compared with only 37% available from vascular plants (Small et al. 1990).

Despite these significant changes in the carbon budget, stable isotope analyses indicated that salmonid food webs remain closely linked to vascular plant detritus and benthic diatoms (Figure 8c). This link is most likely maintained through consumption of prey resources produced in wetlands and other shallow-water habitats (e.g., Figures 5 and 12). A comparison of carbon sources currently utilized with their estimated availability in the estuary indicates that contemporary salmon may select disproportionately for food webs linked to vascular plants and benthic diatoms (Figure 18). Although not

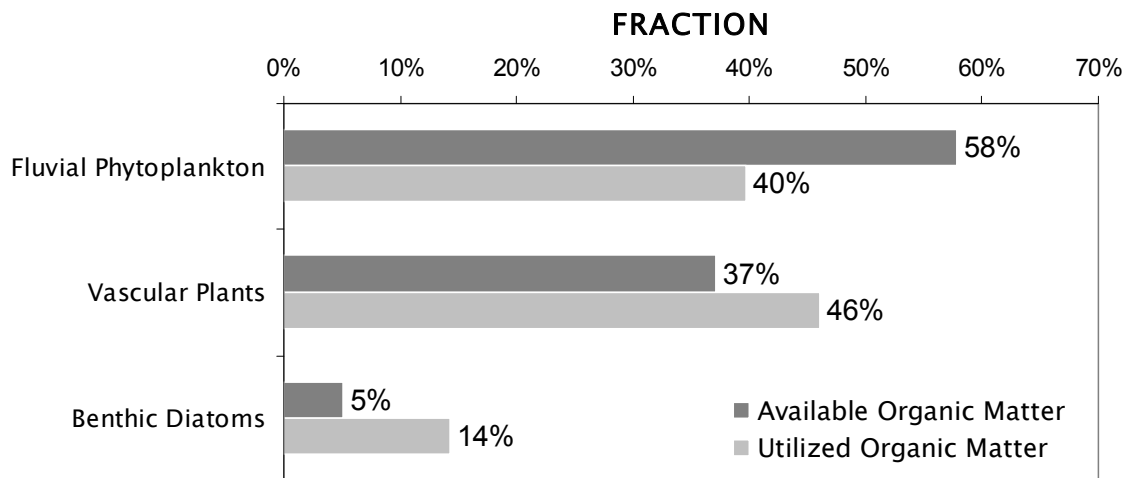


Figure 18. Comparison from mixing model results of available organic matter from estimates of total production (mg C year⁻¹) to the organic matter utilized by subyearling Chinook salmon. Estimates of production are from Small et al. (1990) of 1980 conditions in the Columbia River estuary.

conclusive, these results reinforce the hypothesis that many juvenile salmon may not benefit directly from the enhanced phytoplankton production in mainstem reservoirs, and that the substantial reduction in macrodetrital sources through wetland loss could undermine estuarine capacity to support juvenile salmon (Bottom et al. 2005).

Estuarine Water Temperature

An analysis of long-term temperature records at Bonneville Dam indicated that historical changes in river temperature could further constrain salmon habitat opportunity in the estuary during summer and fall months. Incoming river water exerts a primary influence on water temperatures, and therefore on the availability of suitable rearing habitats, throughout the tidal freshwater portion of the estuary (i.e., above the cooling effects of incoming ocean water). Since the 1940s, shifts in the Pacific Decadal Oscillation and changes in river management together have influenced long-term temperature trends at Bonneville Dam (Figure 19).

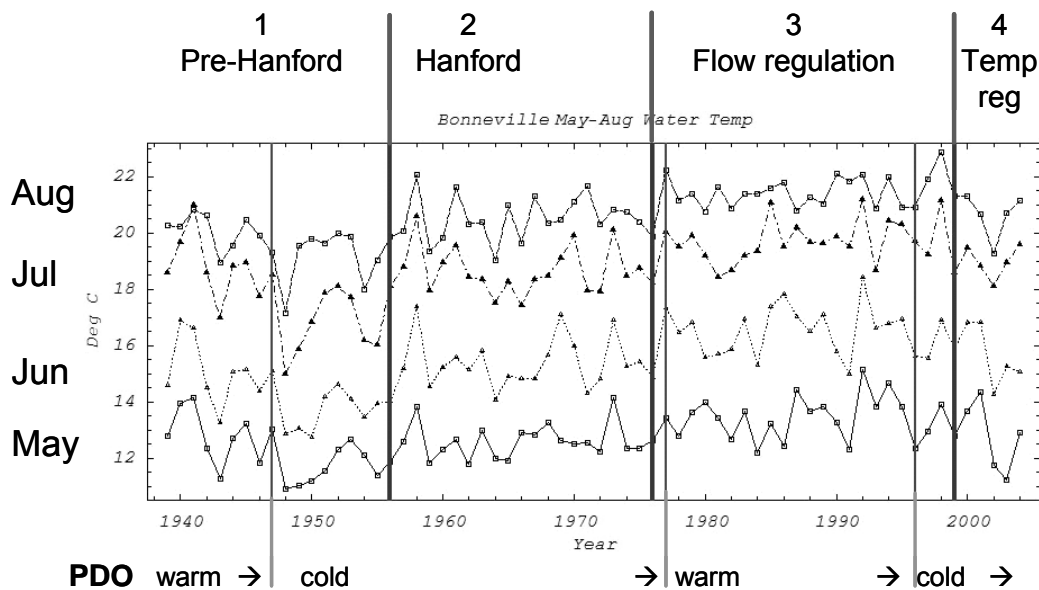


Figure 19. Trends in mean monthly temperatures at Bonneville Dam, May through August. Trends are shown for warm and cold phases of the Pacific Decadal Oscillation and for four river-management eras: 1) Pre-Hanford, 2) Hanford, 3) Flow regulation, and 4) Temperature regulation.

For example, during a cool phase of the PDO that began in the late 1940s, Bonneville temperatures remained relatively low, despite any warming effects from discharges by the Hanford nuclear reservation (management period 2). On the other hand, temperatures increased in the late 1970s through 1990s as the shift to a warm PDO coincided with effects of reservoir heating and flow regulation from a fully developed hydroelectric system (management period 3). Since approximately 1950, mean river temperatures at Bonneville have gradually increased and for the last several decades often have approached or exceeded 20°C by July or August, increasing the bioenergetic demand for juvenile salmon and perhaps limiting availability of suitable estuarine rearing habitat (see Figure 4). The long-term trends raise concerns about future salmon rearing opportunities in the estuary.

Chinook Salmon Life History

We analyzed recent beach-seining results to evaluate the hypothesis that life history diversity of juvenile Chinook salmon in the Columbia River estuary has declined relative to the patterns observed during Rich's (1920) survey more than 90 years ago (Burke 2005; Bottom et al. 2005). Our recent data (Figure 2 and 3) suggested that the influx of fry during spring and summer was somewhat greater than expected from the SARE results (Bottom et al. 2005). Nevertheless, fry abundance in early spring still may be considerably less than Rich (1920) observed in 1916. In contrast to the short estuarine residence times previously reported from an analysis of hatchery-release groups (Dawley et al. 1986; Bottom et al. 2005), our otolith and mark-recapture results (i.e., Figure 11) confirm that many contemporary Chinook salmon continue to express estuarine-resident life histories similar to those reported by Rich (1920; Bottom et al. 2005).

However, beach-seining surveys since 2002 indicated that proportionally fewer juvenile salmon now utilize the estuary throughout the late summer and fall. Unlike the protracted and relatively even pattern of estuary occupation by salmon observed in 1916 (Rich 1920; Figure 20), the population curve is now skewed toward the period March through July and peaks sharply in spring or early summer. This trend is consistent with the hypothesis that salmon life history diversity in the lower estuary has been simplified (Burke 2005; Bottom et al. 2005). According to Rich's (1920) survey results, salmon present in the estuary during September-December 1916 consisted of a diversity of life history types, including recent migrants from upriver, as well as individuals that had spent a significant period rearing in the estuary (Burke 2005; Bottom et al. 2005).

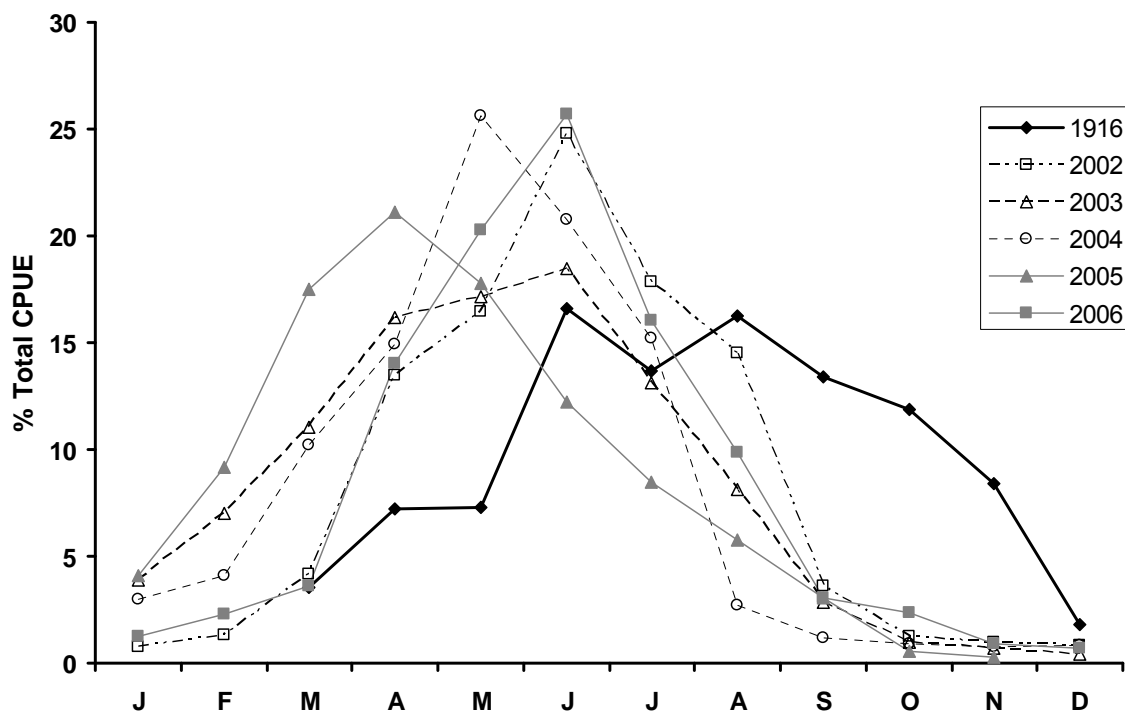


Figure 20. Three-month running average of estimated monthly proportions (percent total catch per unit effort) of juvenile Chinook salmon abundance in the lower estuary, 1916 and 2002-2006. Estuary surveys in 1916 were conducted March-December only.

Assuming Rich's (1920) survey data are representative of the predevelopment pattern of estuary use by juvenile salmon, changes in the abundance curve could reflect reduced habitat opportunities (e.g., Figure 4). These changes could also indicate increased mortality in the estuary during summer and fall, upriver habitat loss, hatchery releases, or hydropower effects. All or any combination of these factors may have contributed to a simplified population structure and altered life history in downstream migrants. The predicted consequences of global warming for the Columbia River Basin (ISAB 2007), that is, reduced snow pack, reduced summer/fall flow, and increased water temperature, could further erode salmon life history diversity by placing additional constraints on estuarine rearing opportunities, particularly in the summer and fall.

CONCLUSIONS

Our investigations have reinforced many of the conclusions of SARE (Bottom et al. 2005) while offering new details about habitat associations needed to support salmon recovery efforts throughout the basin. Results demonstrate that the estuary contributes directly to life history diversity in Chinook salmon by providing opportunities for all Columbia River ESUs to express a variety of subyearling migrant life histories. Small subyearling Chinook salmon seek shallow-water rearing habitats and occupy a diversity of emergent, shrub, and forested wetlands throughout the lower half of the estuary. Many subyearling salmon interact with wetland-based food webs for weeks or months and grow substantially before entering the ocean.

Preliminary evidence suggests that shallow backwater areas and tributary junctions in the upper estuary similarly may afford important rearing habitats for upper and lower Columbia River stocks (e.g., Baker and Miranda 2006, 2007; LCREP 2007). However, comprehensive understanding of estuarine habitat use by all ESUs will require further investigation of representative reaches and habitat types between rkm 101 and Bonneville Dam.

Our results are consistent with the hypothesis that life history diversity of juvenile Chinook salmon has declined since early in the 20th century. This decline may result from a combination of estuarine habitat loss, the effects of watershed modifications, and the effects of hatchery programs on downstream migrating salmon (Burke 2005; Bottom et al. 2005). Our recent investigations suggest that a relatively small proportion of the juvenile Chinook salmon now use the estuary in late summer and fall compared with the pattern observed by Rich (1920) more than 90 years ago. On the other hand, by sampling a variety of shallow-water habitats and analyzing life histories for a range of size classes, we documented that many juveniles rear in the estuary for longer periods than had been recently reported.

For example, one prior analysis of 16 marked hatchery groups estimated that juvenile Chinook salmon travel from Jones Beach to the river mouth in 6 d or less (Dawley et al. 1986). In contrast, we estimated from otolith analyses that 41% of the fish sampled at one lower estuary beach-seining site (Point Adams Beach) had resided within the brackish portion of the lower estuary from 10 to 219 d prior to capture.

Our genetics results demonstrated that all Columbia River ESUs are capable of expressing estuarine-resident life histories. To the extent that habitat opportunities in the estuary can be restored (and the upriver migration pathways that support

estuarine-resident behaviors are not impaired), we conclude that life-history diversity and resilience of Columbia River salmon populations will benefit. This conclusion is supported by results of recent studies in Oregon's Salmon River estuary, where extensive tidal wetland restoration has expanded the variety of estuarine-resident life histories. This expansion has increased the range of sizes and times of ocean entry among Salmon River juvenile migrants (Bottom et al. 2005) and contributed new survivors to the adult population (L. Campbell and E. Volk, unpub. data).

Our investigations also support the hypotheses that 1) reduced input of macrodetritus from wetland habitat loss in the estuary has undermined salmonid food webs, and 2) such losses are not compensated by enhanced delivery of phytoplankton and microdetritus to the estuary from upriver reservoirs (Sherwood et al. 1990; Small et al. 1990; Bottom et al. 2005). Juvenile salmon throughout the estuary fed on insect prey produced in wetlands and other shallow habitats, and energy flow to salmon was linked to wetland detritus. Moreover, despite substantial declines in wetland detrital sources in the last century (Sherwood et al. 1990), contemporary salmonid food webs appear disproportionately linked to wetland-derived prey.

Loss of a large proportion of historical tidal wetlands and floodplains that provided physical habitat structure and supported macrodetrital food webs thus could limit the estuary's capacity to support juvenile salmon. To further evaluate salmonid food-web linkages in the estuary, we plan additional studies in Grays River, a lower Columbia River tributary where estuarine food webs are not directly influenced by mainstem dams and where considerable amounts of formerly diked wetland habitat has been restored to tidal inundation.

MANAGEMENT IMPLICATIONS

Salmon Recovery and Estuary Restoration

Contrary to traditional assumptions that the Columbia River estuary is primarily a hazardous corridor through which salmon must migrate rapidly to avoid predation (Bottom et al. 2005), our research results indicated that the estuary is a productive nursery area for stocks throughout the basin. With the likely exception of spring-run fish from interior basin ESUs, which may rarely use shallow estuarine habitats, Chinook salmon from all Columbia River ESUs with subyearling migrant life histories reside in the estuary for extended periods, feed, and grow rapidly before migrating seaward. The importance of the estuary as a transitional environment and nursery ground is reinforced by previous experimental hatchery releases, which documented a higher return among groups of salmon with access to the estuary compared with those that were released directly into marine waters (Solazzi et al. 1991).

Use of the estuary as rearing habitat by stocks throughout the basin suggests that mitigation actions above Bonneville Dam alone will not be sufficient to meet salmon recovery goals. Although extensively altered and degraded in some reaches, the estuary still contributes to population viability by providing a mosaic of alternative rearing opportunities for all Columbia River stocks. Such opportunities expand in time and space the variety of life history strategies within each ESU that can potentially contribute to adult returns. Traditional mitigation strategies designed to improve salmon survival in freshwater do not account for the habitat requirements of downstream migrants, and may have unintended adverse consequences in the estuary. For example, hatchery programs constrict the stock composition, timing, and size distribution of salmon entering the estuary (Dawley et al. 1986), and flow regulation limits fish access to productive tidal floodplain habitats (Kukulka and Jay 2003a,b; Figure 17).

Changes upriver and in the estuary may account for the apparent simplification of juvenile life histories since the early 20th century (Rich 1920; Figure 20) and could further compromise salmon resilience to future natural or anthropogenic change. Effective salmon recovery strategies therefore, must simultaneously address watershed and estuarine effects on salmon life history diversity. Among the principal changes that may undercut salmon performance in the estuary are:

- a) Widespread loss of peripheral estuarine wetlands and tidal floodplain habitats due to diking, filling, and flow regulation.

- b) Concentration of salmon abundances and life histories through intensive hatchery production and through spill, bypass, and transportation operations that constrict downstream migration opportunities.
- c) Increased mainstem temperatures (from climatic changes and heating of mainstem reservoirs) that may reduce salmon rearing opportunities in the tidal freshwater zone.

Integrated watershed-estuary recovery strategies thus are needed to account for the physical and biological interactions that now limit both habitat opportunities and juvenile life history expression within the estuary.

Our results imply that a primary objective of salmon management and habitat restoration in the estuary should be to increase the diversity, extent, and spatial distribution of habitats capable of supporting multiple salmon ESUs and life history types. Subyearling and yearling migrants exhibit different rearing behaviors and select different habitats within the estuary. Subyearling migrants utilize the entire diversity of shallow-water, wetland ecosystems that we have investigated to date (rkm 35-101), and on average, individuals interact with wetland-based food webs throughout the estuary for periods of weeks to months.

Recovery efforts should encompass the entire habitat continuum, not just sites in the lower estuary, where most research and restoration activities have been focused. Although stable isotope analysis could discern no obvious differences in habitat and food-web pathways among ESUs, the genetic data provided evidence that broad temporal and spatial patterns of habitat use across the entire estuarine tidal gradient (to Bonneville Dam) may vary among stock groups. For example, recent genetic data suggest that a large proportion of Interior Summer/Fall Chinook salmon stocks utilize the upper estuary (LCREP 2007). At the same time, these stocks were found in deltaic wetlands within the Willamette River channel (LCREP 2007) and in lower-estuary wetlands in Cathlamet Bay (Figure 14). To maintain viable Columbia River populations, a comprehensive restoration strategy should encompass habitat opportunities for the full range of salmon life history types and ESUs, including suitable rearing habitats to support salmon migrations through the estuarine tidal gradient.

Today, restoration projects in the Columbia River estuary are chosen primarily through an ad hoc and site-by-site selection process based on land availability and the willingness of landowners to participate. A more strategic approach is needed to direct limited recovery resources toward those geographic areas, habitats, and activities that will most benefit multiple salmon ESUs along the estuarine continuum. Collectively, individual actions should restore connectivity of the estuarine habitat mosaic for juvenile salmon. Furthermore, rather than simply creating or rehabilitating habitat structure, restoration should re-establish ecological processes that rebuild and maintain the habitat mosaic.

To support these goals, historical and contemporary data suggest that a high priority should be given to emergent and scrub/shrub forested wetlands and shallow backwater areas along peripheral shorelines, particularly in the oligohaline and tidal freshwater reaches of the estuary. Dike removal and setbacks are more likely to re-establish functional habitat-forming processes than tidegate replacements or artificial habitat creation projects, provided flow conditions are sufficient to inundate target areas and allow access by juvenile salmon. Fine-scale modeling may be needed to evaluate the restorative potential of various actions within specific upper-estuary locations, which are now strongly impacted by the hydrosystem managed flow regime.

A comprehensive plan is needed to define the goals of estuary-wide restoration and to analyze the potential costs and benefits of alternative strategies for achieving these goals. The present ad hoc approach to estuary restoration—planned and applied entirely at the local scale and focused narrowly on total numbers and acres of projects—does not account for the geographic placement, landscape structure, or connectivity of habitats that are necessary to support the varied migration and rearing behaviors of diverse Columbia River stocks. Our analysis of historical habitat distributions; improved modeling of habitat-opportunity dynamics; and a recent classification of estuarine reaches, habitat types, and complexes (see Leary et al. 2007) provide useful tools and guidance to begin evaluating landscape-scale restoration alternatives throughout the estuary.

Estuarine Research Needs

Additional research is needed to fully document the historical and contemporary diversity of juvenile salmon habitat types, habitat functions, and life histories in the Columbia River estuary. Since 2002 we have documented widespread use of the lower estuary and portions of the mid-estuary, including diverse wetland types and selected shallow beach-seining sites from the mouth to Lord Island (rkm 101). However, salmon-habitat associations in the upper estuary rarely have been investigated. The uppermost forested/scrub/shrub wetlands that we surveyed at Wallace and Lord Islands were among the most heavily used by juvenile salmon and supported juveniles with a smaller size range than that of the lower estuary wetlands.

Other recent studies of upper estuary wetlands were conducted further upstream in the lower Willamette and East Fork Lewis Rivers (Baker and Miranda 2006, 2007). Their results indicate that the timing of occupation and species composition of these tidal floodplain wetlands may differ from the typical March through July pattern we observed for Chinook salmon in lower mainstem emergent marshes. For example, most juvenile Chinook and coho salmon entered these wetlands from late fall through March, often timed with high-water events, and most left during spring runoff in April and May.

These findings raise additional questions about salmon-habitat associations and requirements between rkm 101 and Bonneville Dam, including the following:

1. Do tidal freshwater wetlands and shallow backwater areas of the upper estuary function similarly to those in the lower and mid-estuary?
2. How do marked differences in tidal range and water level fluctuation (including effects of flow regulation) affect habitat access, habitat utilization, and performance of juvenile salmon in the upper estuary?
3. Do peripheral and deltaic wetlands at tributary junctions function similarly or differently from the island/wetland complexes investigated to date in the lower mainstem estuary?
4. Are the deltaic habitats of tributary streams in different reaches of the estuary used widely by salmon from remote ESUs or primarily by local populations?
5. Does flow regulation limit options for restoring wetland habitat opportunity or functionality in the upper estuary?

Although our results describe somewhat different temporal patterns of estuarine migration among ESUs, the spatial distribution of diverse genetic stock groups has not been fully resolved. Preliminary genetic data for a few upper estuary sites (Leary et al. 2007) imply that a much broader sampling effort is essential to compare estuarine life histories among genetic stock groups. We recommend a series of estuary-wide surveys be conducted during selected migration periods to compare the genetic origins of juvenile salmon in representative estuarine reaches from the river mouth to Bonneville Dam. The results would provide a fundamental screening of stock-specific distributions and help to identify key habitat complexes and concentrations of biocomplexity for designing more detailed salmon-habitat investigations in the upper estuary. West Coast laboratories (Seeb et al. In press) continue to improve the genetics baseline for Chinook salmon. This increased resolution will enable us to discern the finer details of estuarine-rearing behaviors and habitat requirements of diverse Columbia River ESUs.

The last 5 years of study have contributed substantially to our knowledge of salmon habitat use and life histories in the lower and mid-estuary. However, this brief study period does not provide an adequate baseline for detecting long-term changes or interpreting their causes. Estuarine habitats and salmon performance will continue to change in response to ongoing fish-production programs, land-use and development activities, hydropower management, habitat restoration efforts, and a rapidly changing Northwest climate (Mote et al. 2003; ISAB 2007). Juvenile life histories, abundance, size composition, and genetic structure in the lower river provide cumulative indices of the basin-wide response of salmon populations to the Columbia River Basin Fish and Wildlife Program. As research attention shifts to fill important data gaps in the upper estuary, a few indicator sites should be maintained in the lower estuary to monitor the status and trends of Columbia River populations, provide an early warning system for unanticipated problems, and assess the overall effectiveness of recovery actions throughout the basin.

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APPENDIX

Publications of the Estuary Research Team

- Anderson, G. A. 2006. Variations in estuarine life history diversity of juvenile chinook salmon based on stable isotope analysis of food web linkages. M.S. Thesis. University of Washington, Seattle.
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